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EXPERIMENTAL STUDIES IN INSECT PARASITISM. VII. THE EFFECTS OF DIFFERENT HOSTS ON THE PARASITE *TRICHOGRAMMA EVANESCENS* WESTW. (HYM. CHALCIDOIDEA)

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(*From the Zoological Laboratory, Cambridge.*)

THE parasitoid *Trichogramma evanescens* has been reared from more than one hundred different species of hosts. All of those hosts have in common that they are eggs of insects; but they differ greatly in other respects. They belong to six different orders,—Lepidoptera, Diptera, Coleoptera, Hymenoptera, Hemiptera, and Neuroptera. They are the eggs of vegetarian, saprophagous, predacious, and blood-sucking forms. They include large eggs and small; eggs with hard shells and with soft; eggs laid in masses and others laid singly. Among them are eggs that hatch within a few days and others that remain unhatched for several months.

The question must arise whether such widely differing hosts produce parasites that are all exactly alike. The association of *Trichogramma* with its hosts is very intimate. It spends its entire developmental period within them, eating their fluid contents and pupating in their empty shells. The parasite is simply the host transformed. Should not one expect individual parasites to be influenced by the particular hosts in which they have developed?

The purpose of this study is to discover what effects, morphological, physiological, and behaviouristic, are impressed upon *Trichogramma evanescens* by the different hosts in which it can develop to the adult stage. The effects of hosts in which the parasite is unable to complete its development have been considered in an earlier paper of this series (Salt, 1938) and are here of no concern.

All the parasites used in this investigation came from a pure strain of *Trichogramma evanescens* descended from a single female parent and reared now for more than 260 generations exclusively on eggs of the grain moth, *Sitotroga cerealella* (Oliv.). Except where it is otherwise stated, all the experiments were carried out at 25° C. and 80% relative humidity.

MORPHOLOGICAL EFFECTS.

1. *Effects on the size of the parasite.*

The most marked effect of different hosts on *Trichogramma evanescens* is their influence on the size of the parasite. A simple demonstration of this effect is provided by the following experiment. From a large collection of eggs of *Sitotroga cerealella*, ten of the smallest were selected; and from a similar lot of eggs of *Ephestia kuehniella* Zell., ten of the largest. A female parasite from a pure strain reared on *Sitotroga* was allowed to lay in three of the small *Sitotroga* eggs, then in three of the large *Ephestia* eggs, and finally in two or three eggs of *Agrotis c-nigrum* (L.). The hosts and the parasites that emerged from them were measured. The experiment was repeated fifteen times. The influence of the largest host, *Agrotis*, is obscured by the fact that, while only a single parasite emerged from each egg of *Sitotroga* and *Ephestia*, in only four cases was there a solitary emergent from the eggs of *Agrotis*, which usually yielded two parasites. Nevertheless, the results, arranged in Table I, show that there is a close correlation between the size of the different species of hosts and that of the parasites that emerge from them.

TABLE I.

Average size in mm./10 of individuals of *Trichogramma evanescens* reared from three different species of hosts.

		Number measured	Size of parasite				Size of host	
			Length	Width of				
				head	thorax	abdomen	Length	Diam.
Parents		15	4·1	1·8	1·4	1·5	5·5	2·4
Female progeny from	*Sitotroga*	21	3·9	1·7	1·4	1·4	4·4	2·3
	Ephestia	32	4·7	2·1	1·7	1·7	5·7	3·6
	Agrotis	32	5·1	2·4	1·9	2·1	5·6	6·5
	Agrotis (solitary)	3	5·7	2·7	2·1	2·5	5·6	6·5
Male progeny from	*Sitotroga*	17	4·0	1·8	1·5	1·3	4·4	2·3
	Ephestia	8	4·6	2·1	1·7	1·6	5·7	3·6
	Agrotis	17	5·1	2·4	1·9	1·9	5·6	6·5
	Agrotis (solitary)	1	5·9	2·8	2·2	2·2	5·6	6·5

A table giving the average result, however, fails to show the great range of size that may occur among the progeny of a single parasite when it attacks different hosts. In a particular case, illustrated by figure 1, the parent measured 0·40 mm. in length; her smallest female offspring, from *Sitotroga*, 0·34 mm.; each of her three female progeny from *Ephestia* 0·46 mm.; and her largest offspring, a solitary female from an egg of *Agrotis*, 0·57 mm. These measurements represent the greatest range obtained in the particular set of experiments described, but they are far from indicating the limits of size of *Trichogramma evanescens*. In the course of other work, individuals descended from the pure strain have ranged in length from 0·24 mm. to 0·7 mm. Hase (1925 : 200) obtained a maximum length of 0·9 mm. in the same species.

The preceding experiments show that the size of *Trichogramma* is influenced by different species of hosts. Within a more limited range, the size of the parasite is also affected by large and small individuals of a particular host species. *Sitotroga cerealella* is a suitable host for a demonstration of this fact because examples can be visually selected so different in size that the largest are nearly twice the volume of the smallest. Experiments were conducted as follows. From a collection of fresh eggs of *Sitotroga*, nine large and nine small ones were chosen and were placed in two groups, each of which could be covered by a small glass container $\frac{3}{4}$ inch in diameter and $\frac{1}{4}$ inch deep. A female *Trichogramma* was placed on the group of small eggs and left for 3 hours at

25° C. The parasite was then transferred to the group of large hosts for one hour. On the fifth day, those small eggs which had turned black, and an equal number of black large eggs, were first measured and then isolated in small vials so that the parasite emerging from each should be known. A few hours after their emergence, the parasite progeny were asphyxiated and measured.

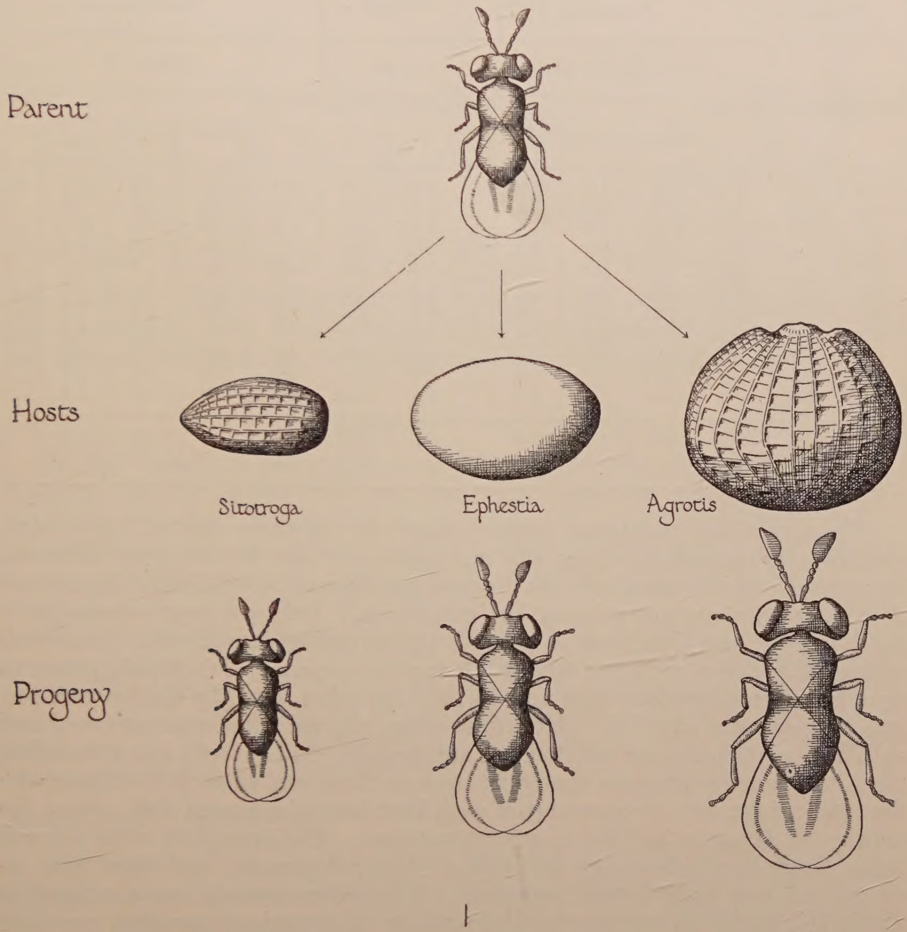

Fig. 1.—Relative size of a female *Trichogramma evanescens* and three female progeny reared from different species of hosts.

The experiment was repeated 15 times but, owing to the reluctance of the parasites to attack very small hosts (see page 92 below), only 18 of the 135 small hosts exposed were parasitised and only 11 gave emergent parasites. The measurements of each of these 11 parasites and their hosts, together with those of an equal number of emergents from large eggs from the same experiments, are set out in Table II. It is clear that the larger hosts produced larger parasites than smaller hosts of the same species.

TABLE II.

Measurements in mm./10 of large and small eggs of *Sitotroga cerealella* and of the individuals of *Trichogramma evanescens* that emerged from them.

Selected small hosts							Selected large hosts						
Hosts		Parasites					Hosts		Parasites				
			Width of							Width of			
Length	Diam.	Length	head	thorax	abdomen	Sex	Length	Diam.	Length	head	thorax	abdomen	Sex
4·2	2·1	3·6	1·8	1·3	1·3	♂	5·4	2·5	4·4	1·8	1·4	1·4	♂
4·4	2·5	4·0	1·8	1·4	1·4	,,	5·8	2·4	4·8	1·9	1·5	1·6	,,
5·0	2·2	4·0	1·8	1·4	1·3	,,	6·2	2·4	4·8	1·9	1·5	1·6	,,
4·5	2·3	4·1	1·7	1·3	1·4	♀	5·8	2·4	4·7	1·9	1·4	1·6	♀
4·7	2·1	3·8	1·7	1·3	1·3	,,	5·8	2·5	4·8	2·0	1·4	1·6	,,
4·7	2·1	4·2	1·6	1·3	1·4	,,	6·0	2·3	4·9	2·0	1·5	1·7	,,
4·8	2·2	4·0	1·7	1·3	1·4	,,	6·0	2·4	4·8	1·8	1·5	1·6	,,
4·9	2·0	4·2	1·7	1·3	1·4	,,	6·0	2·5	4·8	1·9	1·5	1·7	,,
5·0	2·1	4·0	1·7	1·3	1·4	,,	6·0	2·5	4·9	2·0	1·6	1·7	,,
5·0	2·2	4·0	1·7	1·3	1·4	,,	6·0	2·5	4·9	2·0	1·6	1·7	,,
5·2	2·3	4·0	1·6	1·3	1·5	,,	6·2	2·4	4·8	2·0	1·5	1·7	,,
4·8	2·2	4·0	1·7	1·3	1·4		5·9	2·4	4·8	1·9	1·5	1·6	

The eggs of any particular species of host do not range very widely in size, so that solitary parasites from any one species of host are not very different. But eggs of one species of host can produce parasites of very different dimensions if the parasites are not solitary but gregarious. *Trichogramma evanescens* is facultatively gregarious and so permits the following experiment. Into each of two petri dishes were put 50 eggs of *Agrotis c-nigrum.* Ten female parasites were introduced into one dish and 75 into the other, and the dishes were put into an incubator at 25° C. After four hours, the parasites were removed and each of the 100 hosts was isolated in a small vial. On the tenth and succeeding days, the parasite progeny emerged; two or three out of each host from the first dish; four, five, or more out of each host from the second dish, where the density of parasites had led to superparasitism. The emergents were allowed a few hours in which to dry and harden their integument, and were then asphyxiated and immediately measured. The measurements are arranged in Table III, which shows that as the number of gregarious parasites per host increases, the size of the individual parasites is diminished.

It is in cases of superparasitism such as those in the lower part of Table III, where 6 or 7 parasites shared a single host, that the degenerate forms called "runts" appear. These tiny, feeble individuals (fig. 2) occur with increasing frequency as the intensity of parasitism rises. In the experiment described above, no runts emerged from hosts containing two, three, or four parasites; but 4 came from eggs containing five, 7 from eggs containing six, and 12 from eggs containing seven parasites. There can be no doubt, as I shall show later, that runts are produced as a consequence of starvation. Theoretically a solitary runt should emerge from a host that is just too small to support a fully developed parasite. Practically, however, they are seldom if ever produced in this way, for the simple reason that females of *Trichogramma*

TABLE III.

Average size in mm./10 of gregarious individuals of *Trichogramma evanescens* reared from eggs of *Agrotis c-nigrum.*

Number of parasites per host	Size of parasite				Number of parasites measured
	Length	Width of			
		head	thorax	abdomen	
2	4·8	2·4	1·7	1·9	20
3	4·2	2·1	1·5	1·6	15
4	3·9	1·9	1·4	1·5	16
5	3·6	1·7	1·2	1·3	40
6	3·2	1·6	1·2	1·3	18
7	3·1	1·6	1·2	1·2	28

will not lay in such small hosts; and it is only when a host of adequate size is superparasitised that these abnormal individuals appear. Runts represent the ultimate effect on the adult parasite of hosts of too small a size.

2. *Effects associated with size.*

In the foregoing paragraphs a positive correlation has been established between the size of the host and that of its parasite. It follows that any character, whether morphological, physiological, or behaviouristic, that is connected with the size of the parasite must be considered in this paper, because it may be influenced by the host. The physiological and behaviouristic characters will be considered in their places below.

Most of the morphological characters correlated with size in *Trichogramma* have to do with the proportions of the limbs and of the various parts of the body. The influence of the host on these is proportional to its influence on gross size, and the effects are so self-evident as to need no particular study. There are one or two effects, however, that are less obviously a matter of stature and that are worthy of brief mention.

(*a*) *Trichiation of the wings.*

The wings of *Trichogramma* are adorned with numerous hairs, of which the larger, or macrotrichia, are arranged in nine principal rows. The effect of different hosts on the number of macrotrichia in these rows has been studied by Oldroyd and Ribbands (1936), using my pure strain of *Trichogramma evanescens* and its F_1 progeny reared from the eggs of several Lepidoptera. These workers have demonstrated a very close correlation between the number of macrotrichia in the rows and the length of the wing (their figure 2), and have shown that both of these are positively correlated with the size of the host from which the parasite emerged.

(*b*) *Hairiness of the male antennae.*

The flagellum of the antennae of the male *Trichogramma evanescens* bears numerous long hairs which are a conspicuous characteristic of the sex. The length of these hairs remains relatively constant, being always greater than that of the scape, but the number varies with the size of the animal. Ten antennae of males reared from *Sitotroga* were found to have an average of about 30 long hairs, while the antennae of larger males reared from *Agrotis* had an average of 37 hairs.

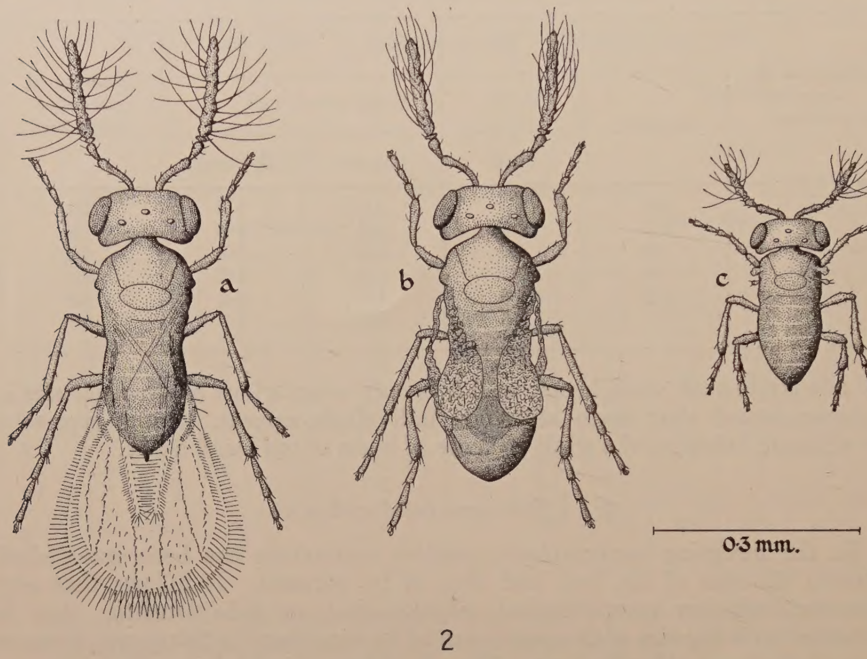

FIG. 2.—*Trichogramma evanescens* Westwood. A, normal male; B, normal male just emerged, with the wings unexpanded, the antennal hairs appressed, and the meconium not yet cast; C, male runt.

3. *Effects apart from size.*

In *Trichogramma evanescens* there are apparently no morphological effects of the host upon the parasite apart from those associated with size. In a related species, *Trichogramma semblidis* (Auriv.), it has recently been shown that one particular host, *Sialis lutaria* (Fab.), has the peculiar effect of eliciting a normal apterous form of the male, quite different in several characters from the ordinary winged male (Salt, 1937). Eggs of *Sialis lutaria* had not that effect on the few individuals of *T. evanescens* that were successfully reared from them (Salt, 1939), and no similar apterous form of *T. evanescens* has ever been proved to exist.

This has to be emphasised because several authors have in the past referred to apterous males of *T. evanescens*. It appears, however, that they had either confused the two species, *evanescens* and *semblidis*; or had not given the newly emerged parasites time to expand their wings (fig. 2, B); or else had looked upon the runts of *evanescens* as the equivalent of the apterous forms of *semblidis*. But runts are not at all normal forms. Four considerations indicate that they are degenerate individuals produced by starvation. They do not occur in uncrowded cultures but are always associated with superparasitism. They are invariably very small (0·24 to 0·33 mm. long). They are so feeble that they live only a few hours and are never able to move actively or, so far as I have observed, to reproduce. All the structural peculiarities that have been ascribed to them (reduction or loss of wings, changes in the antennae) are characters of degeneration and distortion (fig. 2, c). The formation of runts is, indeed, the most striking effect of the host on the structure of *Trichogramma evanescens*, but it is not the appearance of a new apterous form. It is merely the final stage of the reduction in size of the parasite under the influence of an insufficient host.

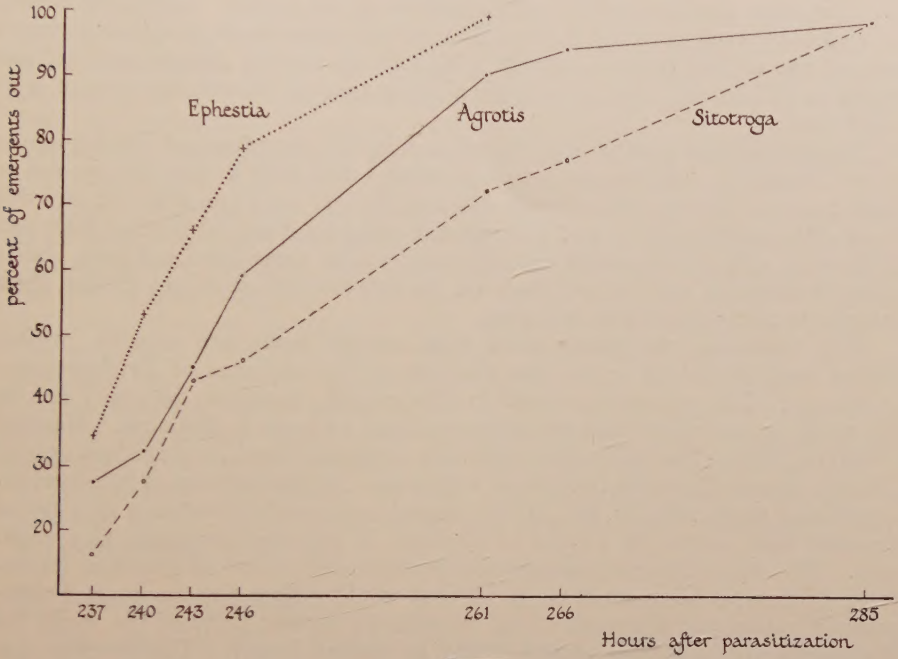

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FIG. 3.—Relative time of emergence of individuals of *Trichogramma evanescens* reared on three species of hosts.

PHYSIOLOGICAL EFFECTS.

1. *Effects on the rate of development.*

The influence of temperature and other physical environmental factors on the rate of development of insects is now thoroughly appreciated, but the effects of biotic factors are only just beginning to be realised. In the case of parasites, the host is one of the environmental factors that must be considered. This is demonstrated by observations made in the course of the experiment described on page 81. In that experiment, the progeny of 15 females of *Trichogramma evanescens* were reared on three species of hosts, *Sitotroga*, *Ephestia*, and *Agrotis*. The time of parasitisation was known within a few minutes; the parasitised hosts were kept together under identical and controlled environmental conditions; and the time of emergence of the parasites was recorded. The earliest progeny appeared 236 hours and the latest 285 hours after parasitisation. In eggs of *Ephestia* the average developmental period was 243 hours; in *Agrotis* 250 hours; and in *Sitotroga* 256 hours. When the emergence of the parasites from these three hosts is plotted against time (fig. 3), it is apparent that the parasites emerged from eggs of *Ephestia* earlier than they did from eggs of either *Agrotis* or *Sitotroga*.

The reason for this has not been deliberately investigated, but several observations suggest that two factors may be concerned : (1) Eggs of *Ephestia* have a thinner chorion than those of either *Sitotroga* or *Agrotis* so that the young adults may be able to bite a way out of them more easily. (2) *Ephestia* eggs may provide the optimum amount of food for rapid emergence, while *Sitotroga* eggs provide too little and *Agrotis* eggs too much. That there is such an optimum is suggested by the fact that solitary individuals in *Agrotis* required an average of 262 hours to emerge; individuals sharing *Agrotis* eggs in twos required 247 hours; and individuals sharing them in threes emerged in only 244 hours.

Eggs of *Galleria mellonella* (L.) seem to delay the emergence of *Trichogramma* very noticeably. On the one occasion when I was able to use this species as host, many of the parasitised eggs did not blacken until the 6th, 7th and 8th days after parasitisation, and the parasite progeny emerged on the 13th and 14th days, although *Ephestia* eggs attacked at the same time and kept beside them in the same dish turned black on the 4th and 5th days and yielded their emergents normally on the 10th day.

The foregoing paragraphs show that certain hosts are capable, within rather small limits, of influencing the rate of development of *Trichogramma evanescens*. The principal interest in this subject, however, naturally lies in the much greater effect that might be produced by hosts in diapause. Marchal (1936) has shown that when *Trichogramma cacaeciae* March. is reared on eggs of *Cacoecia rosana* (L.) while they are in a diapause, its development is inhibited for a period of seven months, but, if it is reared on eggs of *Ephestia* or on eggs of *Cacoecia* that are not in a state of diapause, it goes on developing at a rapid rate. This is a matter of considerable interest and is also of practical importance because, if hosts could be found that would induce a diapause in *Trichogramma evanescens*, shipment of the parasite to various parts of the world for the practice of biological control would be rendered easy. The problem has therefore been studied during two seasons, using as hosts the following species of Lepidoptera.

(a) *Polia flavicincta* (Fab.).

The eggs are laid in August and September and hatch the following April. They are yellow when laid but turn brown during the first few days owing to the formation, inside the colourless chorion, of a dark membrane (the serosa) which surrounds the yellow yolk. This process is complete on the fifth day and then, as shown by weekly dissections, the egg remains without further development during the winter. That the eggs are actually in a state of diapause is indicated by the fact that whether they are kept during the autumn and winter at natural temperatures or at a constant temperature of 25° C., they do not hatch until the spring.

For experiments on parasitism, the eggs of a fertile clutch were divided into nine groups. One group was exposed to parasitisation on the day the eggs were laid, and succeeding groups when they were 7, 14, 21, 28, 35, 39, and 46 days old. The eggs were readily parasitised and in every case the parasite progeny developed at once and emerged normally 10 or 11 days after parasitisation. The ninth group, which was unparasitised, hatched the following spring. The eggs of *Polia flavicincta*, then, although themselves in a diapause, did not induce a diapause in the parasite *Trichogramma evanescens*.

It may be mentioned in passing, that eggs laid by an unmated *Polia* female, which were infertile and therefore never would have hatched, were successfully parasitised and yielded emergent parasites at the normal time.

(b) *Epineuronia popularis* (Fab.).

The eggs of this species are laid in September and hatch in the following spring, so that its habit appears similar to that of *Polia*. The similarity is only superficial. The embryo of *Epineuronia* develops rapidly, so that 14 days after the egg was laid the larva is almost fully formed, and after 28 days the larva is completely developed and can move within the egg-shell. Kept during the winter at 25° C., a number of these larvae never emerged and eventually died, but others kept at natural temperatures hatched the following March. *Epineuronia*, therefore, passes the winter in a true diapause which is apparently of the egg but actually of the first-instar larva within the egg-shell.

Eggs of *Epineuronia* were parasitised on the day they were laid and others at 19 days of age, and both groups yielded parasite progeny after 10 days. It may be claimed, however, that these hosts were still developing and therefore not yet in their diapause. Other hosts, however, were exposed on the 32nd day when the host larvae were fully formed and presumably in a state of diapause, and a single parasite progeny emerged 11 days later. It is unfortunate that there were not more emergents from this experiment, but the female parasites were disturbed in the act of laying by the movements of the fully developed host larvae inside the eggs (*cf.* Salt, 1938 : 236) and in most cases they withdrew immediately after penetrating the egg-shell and went off without actually parasitising the host. No additional parasites emerged the following spring; and it is certain, at any rate, that no diapause was induced in *Trichogramma* by this host.

(c) *Xanthorhoe didymata* (L.).

This species is said to pass the winter in the egg stage. A few eggs laid on 9th August contained fully developed larvae when dissected on 12th September; so that, if the statement is true, there must be a diapause of the first-instar larva, as in *Epineuronia*. Some of the eggs were exposed to *Trichogramma* on 31st August and yielded parasite progeny on 14th September.

(d) *Orthosia gilvago* (Esper).

This late-flying noctuid is supposed to hibernate in the egg stage. Eggs laid on 21st October and kept at room temperature during the winter shrivelled and never hatched. Eggs of the same clutch exposed to *Trichogramma* on the day they were laid and then kept at 25° C. gave parasite progeny on the 10th day.

It would obviously have been desirable to rear *Trichogramma evanescens* on *Cacoecia rosana* in order to discover whether that host has the effect on the parasite that it has on *T. cacaeciae*. Unfortunately, in spite of attempts extending over two seasons, I have never been able to experiment with eggs of *C. rosana*. Marchal (1936 : 516–19) says that his strain of *T. evanescens* would not attack eggs of *Cacoecia* in diapause, and that when it attacked fresh eggs, no progeny developed.

No host, then, has yet been found which induces a diapause in *Trichogramma evanescens* as *Cacoecia rosana* does in *T. cacaeciae*. This matter is discussed below.

2. *Effects on vigour.*

Large individuals of *Trichogramma* appear stronger and more vigorous than small specimens. In order to translate this appearance into objective data, it is necessary to measure the rate at which some physical activity is performed. Rate of movement would serve; but a more convenient activity for measurement is that of oviposition. It has been shown elsewhere (Salt, 1938 : 224) that the shells of some hosts offer considerable resistance to the ovipositor of the parasite, and are pierced only after arduous drilling that lasts for several minutes. The time required to drill through the chorion of the host, therefore, will serve as an indication of the strength of the parasite.

Experiments to measure the strength of parasites reared from different hosts were performed as follows. A female parasite was first allowed to attack two eggs of *Sitotroga*, since young females do not always drill efficiently on their first host. They were then presented successively with four different species of hosts—*Sitotroga cerealella*, *Ephestia kuehniella*, *Agrotis pronuba* (L.), and *Hydriomena bilineata* (L.), in that order—and were allowed to attack two of each of them. Each attack was observed under a binocular-dissecting microscope and the time between its beginning and the penetration of the host, that is, the total time occupied in drilling through the chorion, was measured with a stop-watch. Immediately after completing its series of ovipositions, the female was asphyxiated and measured. The experiment was repeated fifteen times, five times with small females emerged from eggs of *Sitotroga*, five times with middle-sized parasites from eggs of *Ephestia*, and five times with large females from eggs of *Barathra brassicae* (L.). The results, summarised in Table IV, show clearly that the time required to penetrate the chorion of the host varied inversely with the size of the parasite. One may say, then, that the large females emerged from *Barathra* were stronger than those from *Ephestia* and these latter than the small females reared from *Sitotroga*.

Table IV.

The average time required by parasites from three different hosts to drill through the chorion of four species of host eggs.

(Each time quoted is the average of ten observations.)

Parasite from		*Sitotroga*	*Ephestia*	*Barathra*
Average length in mm./10 . . .		4·2	4·7	5·2
Time required to drill through	*Sitotroga* . . .	1′ 14″	1′ 1″	50″
	Ephestia . . .	44″	36″	32″
	Agrotis	1′ 34″	1′ 31″	1′ 2″
	Hydriomena . . .	13′ 52″	10′ 30″	7′ 14″

The time required to pierce the chorion of a host is a test of the strength of a parasite. The time required to perform a succession of such acts will serve as an indication of its vigour. During the last few years many experiments have been performed in which females of *Trichogramma* were allowed to oviposit in a number of hosts under observation, the time of each act being carefully recorded. From the notes of such experiments as are comparable for my present purpose, it appears that small parasites, emerged from eggs of *Sitotroga*, required an average of 66 minutes to find, examine, penetrate, and parasitise

10 hosts; while large parasites, emerged from eggs of *Agrotis*, required only 37 minutes. These experiments were not designed as a demonstration of vigour but they serve to indicate what is readily apparent to an observer, that large parasites are much more vigorous than small ones in the various movements involved in seeking and parasitising hosts.

That the host affects the strength and vigour of its parasite through the effect on size is clear. It must not be assumed, however, that the host affects the physiology of its parasite *only* through the effect on size. Some hosts produce quite large parasites which are nevertheless extremely feeble. The few individuals of *Trichogramma evanescens* that have been reared from eggs of *Sialis lutaria*, for instance, were of good size, but they were very weak and inactive. They moved slowly, rested often, and, whether through weakness or disinclination, did not attack any hosts. *Sialis lutaria*, however, is a host normally unsuitable for *Trichogramma evanescens* (Salt, 1938 : 231) so that the problem merges at this point into that of Host Suitability and passes out of the scope of the present paper.

3. *Effects on longevity and fecundity.*

The weakness of specimens of *Trichogramma evanescens* reared from eggs of *Sialis lutaria* has been mentioned. These individuals were not only feeble, they were also very short-lived. Of the 20 that were reared from that host, 17 died within 12 hours of emergence and only one lived longer than a day. None of them was able to reproduce. It may be said, therefore, that the host can directly affect the longevity and fecundity of its parasite.

The host can also affect fecundity through the effect on size. Flanders (1935 : 177) says that large specimens of *Trichogramma* (? species) may be over five times as prolific as small ones. Published data (Salt, 1935 : 417) show that individuals of *T. evanescens* reared from *Ephestia* laid more eggs in an 8-hour period than did the smaller individuals reared from *Sitotroga*; and unpublished experiments indicate that large parasites from eggs of *Agrotis* have a much higher reproductive rate.

As for longevity, the adults of *Trichogramma* that in my experience have lived longest were a number of large specimens emerged from eggs of *Agrotis*.

It was my intention to include here mortality curves and data on fecundity for parasites of different sizes, but circumstances have prohibited the experiments that were planned for this part of the paper.

BEHAVIOURISTIC EFFECTS.

The host from which a female *Trichogramma* emerges does not appear to condition the parasite to seek hosts of the same species for its progeny. This fact was first pointed out by Hase (1925 : 186), who allowed females of *Trichogramma evanescens* reared from various insect eggs to choose hosts for their progeny, and found that they showed no preference for the species from which they had themselves emerged. It has since been shown (Salt, 1935 : 417) that a pure strain of *T. evanescens* reared for 63 generations exclusively on eggs of *Sitotroga* did not develop in that time a preference for its accustomed host but, when given the choice, still preferred to attack eggs of *Ephestia*. Recent experiments show that this pure strain still chooses eggs of *Ephestia* or *Agrotis* in preference to those of *Sitotroga* although it has now for more than 260 generations had experience of no host other than *Sitotroga cerealella*.

Nevertheless, the host does influence the selective behaviour of its parasite, although only indirectly, through the effect on size. In a previous paper of this series (Salt, 1935) it was demonstrated that the size of the host is an important factor in determining its acceptability to *Trichogramma evanescens*. Among additional data now accumulated on this subject, but not yet published, one is of particular concern here. It is, that the minimal size of host acceptable to a parasite depends upon the size of the parasite itself. Large parasites do not accept hosts that smaller parasites will readily attack.

Three types of experiments illustrate this fact. In the first type, a large female emerged from an egg of *Agrotis* was placed in a dish with 30 small eggs of *Sitotroga*, and was kept under observation. The parasite was eager to lay and passed from egg to egg, giving each a cursory examination, but almost immediately rejecting it. After a time the parasite lost interest in the small hosts, and moved away from them towards the sides of the dish but, by manipulation of the dish with regard to light and gravity, it could be led to them again. After half an hour, every egg had been found at least once; but none had been accepted or had even evoked a careful examination. The parasite was then removed to a dish of *Agrotis* eggs. The first it met attracted its complete attention, and was accepted; proving that the female was eager to lay. The parasite was allowed to oviposit in 3 or 4 eggs of *Agrotis* and was then put back for a quarter of an hour into the dish of small *Sitotroga* eggs, which it again refused to attack. This experiment was repeated four times with identical results. The four large parasites did not accept a single small host.

In the second type of experiment, two dishes were prepared, each containing 25 small eggs of *Sitotroga*. Into one was placed a female *Trichogramma* emerged from *Sitotroga*; into the other, one reared from an egg of *Agrotis*. The dishes were put into an incubator at 25° C. for 4½ hours. The parasites were then removed and the dishes left in the incubator to develop. This experiment was repeated four times. Each of the small parasites from *Sitotroga* eggs accepted and parasitised some of the small hosts, 9, 17, 18, and 20 being parasitised in the four experiments. Only one of the larger females (an individual measuring 0·49 mm. in length) attacked the eggs, parasitising 14 of them. The other three large females did not parasitise any.

In both of the above groups of experiments, the parasite was left with the hosts for only a part of its life. In other experiments a large female reared from *Agrotis* was placed in a dish with 50 small *Sitotroga* eggs, and left at 25° C. until it died, about 36 hours later. This experiment also was repeated four times. One female (0·48 mm. long) parasitised four of the small hosts; the other three parasitised none.

The twelve experiments described are supported by many others of different types. One has been mentioned above (p. 83); Laing (1938 : 296) has recorded another; and Flanders (1935 : 177) has published a similar observation on the American *Trichogramma* that is sometimes called *T. evanescens*. All these observations lead to the same conclusion—that large females of *Trichogramma* usually fail to attack hosts of small size although the latter, which are readily parasitised by smaller individuals, are actually suitable for their progeny.

It follows from all these data that the host, through its effect on the size of its parasite, affects the behaviour of that parasite in regard to the size of the hosts that it, in its turn, will parasitise.

Discussion.

In one sense, this study is a continuation of the preceding paper of this series (1938) dealing with the problem of Host Suitability. In that paper were considered the properties of the host that influence the parasite during its immature stages. It was there observed that some hosts (considered, from the point of view of the parasite, as unsuitable) so affect the young parasites feeding upon them as to prevent their development. In this paper have been considered the properties of the host that influence the parasite in its adult stage. I have here observed that some hosts, although they are themselves destroyed, may affect the adult parasites that emerge from their remains.

The object of this study has been to discover in what characters and to what extent different hosts can influence adults of *Trichogramma evanescens* that have developed upon them. In some respects the search has been disappointing. In a related species, *Trichogramma semblidis*, one host, *Sialis*, so deeply influences the parasite as to alter completely the facies of its male sex (Salt, 1937). In another species, *T. cacaeciae*, the host *Cacoecia rosana* so seriously affects the development of the parasite as to delay its emergence for seven or eight months (Marchal, 1936). No such striking effect of a host has been found in *T. evanescens.*

Two explanations are possible. It may be that only certain hosts have the quality of eliciting a reaction in *Trichogramma evanescens*, as only *Sialis* alters *T. semblidis* and only *Cacoecia* affects *T. cacaeciae.* In that case, a continued search might ultimately reveal a host which would induce a dimorphic form or a diapause or some other striking effect in *T. evanescens.* On the other hand, it may be that the ability to develop a distinct apterous form in *Sialis* is a specific character of *T. semblidis* and the capacity to be influenced to enter a diapause a specific character of *T. cacaeciae*; " specific " in both cases being understood to mean " distinct from *T. evanescens.*" In this case, no host can have the effect on *T. evanescens* that *Sialis* and *Cacoecia* have on their parasites.

The principal effects that different hosts have been found to have on *Trichogramma evanescens* are those concerned with size. This is a rather obvious result. The host is the food of the parasite. According as it is well fed by an ample host or starved by a meagre one, *Trichogramma* is large or small. But it is not merely the stature of the individual that is affected. So far as they are correlated with its size, the physiology and the behaviour of the parasite are also influenced by the host.

Indeed, one of the effects correlated with size—the selection behaviour of the parasite—is perhaps the most interesting that has been found in *Trichogramma evanescens.* I have shown that large parasites emerging from large hosts tend in their turn to parasitise only large hosts, and disdain to attack small hosts that would actually be suitable for their progeny. Small parasites, for their part, have difficulty in piercing the chorion of large hosts and are sometimes quite unable to penetrate them (Salt, 1938 : 225). In effect, these two results tend towards a division of the species into two ethologically isolated strains : one of large individuals unwilling to attack small eggs, and one of small individuals unable to parasitise large ones. Such a difference might in some circumstances be expected to lead to the separation of two distinct forms. Ordinarily, however, two factors oppose that result—the tendency of small females to prefer large hosts and stubbornly to attack them (Salt, 1935), and the habit of large females of laying several eggs in a large host so that the size of their gregarious progeny is much reduced (p. 84 above). These two factors ordinarily prevent the complete segregation of the two strains.

A general consideration of the results of this study raises a matter of fundamental importance. The possibility of progress in quantitative biology depends on the existence of biological constants which, although not necessarily so precise as those of physics and chemistry, are characteristic of particular species. The fecundity of an organism, for instance, is usually considered to be a biological constant. That a litter of kittens should number between 3 and 6 is taken for granted; and there would be consternation at home if the family cat suddenly produced a litter of 250, the average number of young produced at one time by many flies. But I have found that the number of eggs a female *Trichogramma* can lay depends to a very considerable extent on the host from which it emerged. The concept of biological constants seems to be put into doubt by such a study as this, in which not only the fecundity but also many points in the morphology, physiology, and behaviour of an animal species is found to be influenced by a factor, the host, that has already ceased to exist when the observations are made.

The difficulty will be resolved when it is thoroughly understood that the fecundity, for instance, of an organism is not precisely stated by a bare number. A flour moth (*Ephestia kuehniella*, Payne, 1934) may lay 225 eggs at 27° C.; but only 177 at 20° C. under otherwise identical conditions. A fruit-fly (*Drosophila melanogaster*, Pearl, 1932) may lay 12·6 eggs per day when it is in a bottle with one other fly; but only 8·5 eggs per day when it is in an identical bottle with three other flies. To define the boiling-point of a fluid, a physical constant, the physicist must record the pressure at which his observation was made. Similarly, to define the fecundity of an organism, a biological constant, it is essential to record in considerable detail the environmental conditions, physical and biotic, under which it was determined. In many cases one does not even know which of those conditions are important. This study shows that in the case of *Trichogramma*, and probably of other parasitoids, the host is one of the effective factors that must be controlled and stated before biological constants relating to the parasite can have any general validity.

ACKNOWLEDGEMENTS.

On account of the war I have been unable to complete the schedule of work originally planned for this study, and I apologise especially for the sketchy nature of the sections on fecundity and longevity. At different stages of the investigation my cultures of *Trichogramma* have been looked after by E. B. Basden, J. Petchell, and M. V. Brian, whose services were provided by a grant from the Department of Scientific and Industrial Research. Dr. O. W. Richards has on several occasions kindly provided me with eggs of *Agrotis* and *Barathra*. My name must be added to the long list of workers who are indebted to Mr. W. H. T. Tams for determinations of Lepidoptera.

SUMMARY.

(1) The size of individuals of *Trichogramma evanescens* is largely controlled by the size of the hosts in which they develop.

(2) The vigour, the fecundity, the longevity, and the rate of development of individuals of *Trichogramma* are affected by their hosts.

(3) Through its effect on their size, the host influences the behaviour of females of *Trichogramma* selecting hosts for their progeny.

(4) The host is one of the environmental factors that must be controlled in any quantitative work on *Trichogramma*.

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BOOK NOTICE.

Insect pests in stored products. By H. HAYHURST. Photographs by H. BRITTEN. 8vo. London (Chapman and Hall), 1940. pp. 83, 49 pls. Price 15*s.*

This book consists of a series of articles originally published in *Food* from August 1939 under the title "Insect infestation of stored products."

It comprises a list of Insect and Arachnid pests of stored products with some account of control measures. Lists of the products on which each pest has been recorded are given and a description of the larval and adult stage of each pest with an illustration of most of the species.

The book is written "in such a way that any technical man without much entomological knowledge can readily understand and follow it." It is addressed to "those engaged in the transport, the manufacture, the wholesaling and storing of perishable goods, and particularly, of course, food-stuffs."

BOOK NOTICE.

A Survey of insecticide materials of vegetable origin. Edited by H. J. HOLMAN. pp. viii + 155. 8vo. London (Imperial Institute), 1940. Price 3*s.* 6*d.*

This work is issued, under the auspices of the consultative committee on insecticide materials of vegetable origin, by the Plant and Animal Products Department of the Imperial Institute.

The book is arranged in 5 parts dealing with: Alkaloid-containing materials; Plants containing Rotenone and allied compounds; Pyrethrum; Quassia; and Plant oils.

The scope of the book is not restricted to empire sources but the whole of the existing, and in some cases the potential, world sources are surveyed.

The list of references to the literature which is given in the book extends to 372 titles. There is no index to the book but a full table of contents is supplied.

THE REPRODUCTIVE ORGANS OF *SCATOPHILA UNICORNIS* CZERNY (DIPTERA)

By Niels Bolwig, M.Sc., F.R.E.S.

I give here a short description of the reproductive organs of the fly *Scatophila unicornis* Czerny. The study was carried out by simple dissection under a binocular microscope, all the diagrams being made with the help of Bolwig's drawing apparatus. I am indebted to Statens Plantepatologiske Forsøg in Denmark for being allowed to carry out my studies there and to the chief of the zoological department of the laboratory, Dr. P. Bovien.

The Female Reproductive Organs (fig. 1).

The two ovaries consist of two groups of *ovarioles.* The ovarioles unite each side by their anterior end to a *suspensory ligament* by which they are suspended. Each ovariole consists of three parts: a *terminal filament* (t.f.), an *egg tube* and a very short *supporting stalk* or *pedicel.* The principal part is the egg tube, which in its front part contains the *germ cells* (g.c.), the *germarium* (germ.), and behind these the derivatives of the germ cells: the *follicles* (fol.). The terminal filament continues from the anterior end of the egg tube and is a part of the suspensory apparatus of the ovary; the pedicel is the short ovariole duct uniting the egg tube with the *lateral oviduct.*

The covering of the ovariole is a thin structureless membrane, known as the *tunica propria* (t. pr.) which stretches over the terminal filament, the egg tube and the pedicel. No epithelial sheath is seen outside the tunica. The germ cells form a mass of cells in the front part of the egg tube. These cells form the follicles. In the posterior end of the *germarium,* little groups of cells (r.c.) are seen to be surrounded by elongated, cigar-shaped cells. The elongated cells form the *follicle cells* (fol. c.). Their nuclei are elongated like the cells themselves and they are dark. The little group of rounded cells is the *oöcyte* (oö.) and its *nutritive cells* (n.c.). The nutritive cells seem to be of germ cell origin. The oöcyte and its nutritive cells are produced by division of a single cell, the *oögonium.* Farther down the egg tube, the follicle cells form a single layer of cubical cells with dark rounded nuclei. Their number increases gradually as the follicle glides down through the tube. The rounded cells and their nuclei increase in size, the nuclei getting paler. In the posterior end of the tubuli, one of the rounded cells increases enormously and its plasma gets white and filled with yolk. Only a tiny bit of clear plasma surrounds the nucleus that remains in the anterior end of the egg. This cell is the *oöcyte* (oö), later the egg. When the oöcyte begins to increase in size, the follicle cells in the anterior end of the follicle flatten and soon after they die. The follicular cells surrounding the oöcyte stretch and form a columnar epithel. Later on they flatten too and die. The posterior end of the egg tubes appears to contain a little group of cells that forms a *plug.* The nutritive cells degenerate and form a *shield* (sh.) that covers the front part of the egg. When the egg is fully formed, the epithelium of the chamber begins a secretory activity producing a substance which is discharged upon the egg and hardens to form the egg shell. This shell is the chorion (chor.). On its outer surface, the chorion retains the marks of the cells that produced it, in the form of honeycomb patterns of fine ridges reproducing the outlines of the cells of the follicular wall. The follicle cells cover the whole surface of the egg, with the exception of the front part which is covered by the degenerated nutritive cells. The pedicel is extremely short. A pair of lateral oviducts lead behind from the ovaries. They unite in an *oviductus communis* (od. c.). The posterior opening of the oviduct is the female gonopore. On the ventral side of the oviductus communis a little, double-walled, bottle-shaped *spermatheca* (sperm. th.) is seen. The spermatheca is darkly pigmented. The wall of the lateral oviducts, as well as the wall of the oviductus communis, is provided with an outer layer of circular muscle fibres and an inner layer of longitudinal muscle fibres. The gonopore (figs. 1 and 2, gon. p.) is situated between two little oval plates (val. 1) apparently behind the seventh sternite—but in reality

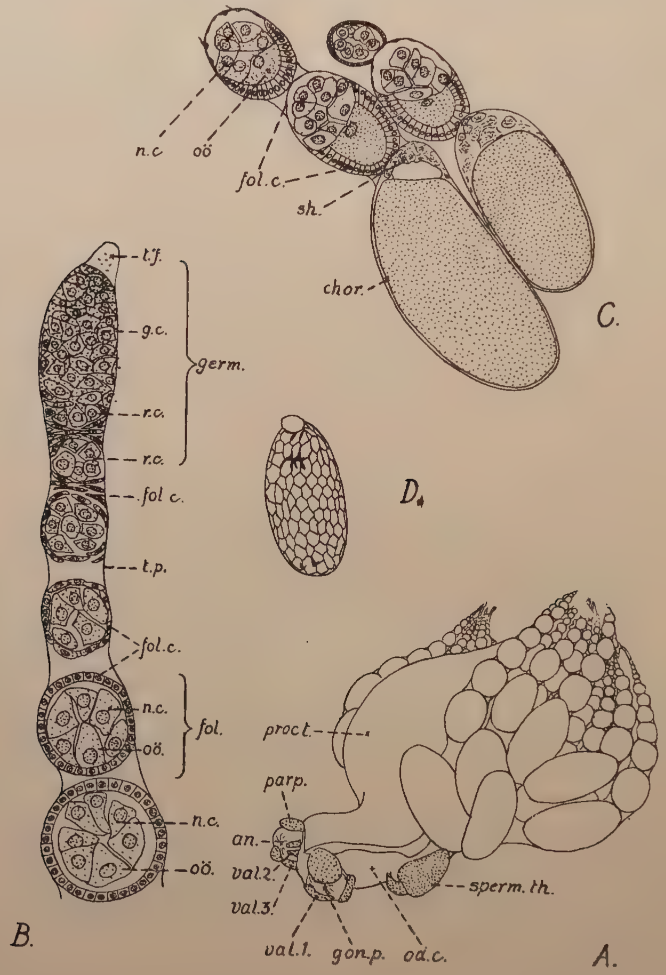

Fig. 1.—*S. unicornis* Czerny, ♀ reproductive organs. *A*, ovary; *B*, ovariole, upper part; *C*, ovariole, lower part; *D*, egg.

behind the eighth segment—however, the whole eighth segment, and the segments following as well, are rudimentary. The eighth and ninth segments are seen only as two fine ridges surrounding the rear end of the abdomen; one in front and the other behind the gonopore. In connection with the second ridge are to be seen three little, weakly chitinised, ventral lobes; two lateral (val. 3) and one median (val. 2). Probably the two lateral lobes (val. 1) of the gonopore are homologous with the first valvulae of the ovipositor of other insects. Similarly, the median lobe of the ninth segment (val. 2) is probably homologous with the second valvulae and the lateral one (val. 3) with the third valvulae of the ovipositor of other insects. Behind the three little lobes, and between a pair of oval paraprocts (parp.), the anus (an.) is to be seen.

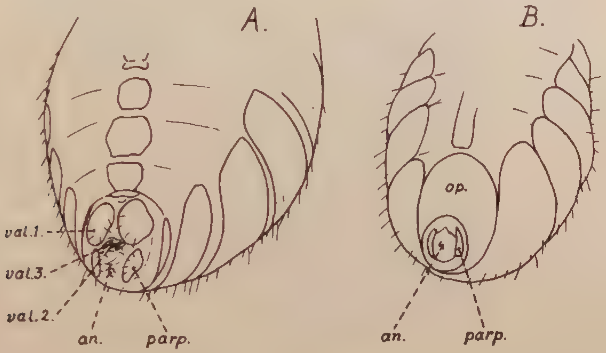

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Fig. 2.—*S. unicornis* Czerny. Underside of end of abdomen. *A*, ♀; *B*, ♂.

The Reproductive Organs of the Male.

The outer genitalia (figs. 3 and 4) of the male are minute. They are covered by a little strongly chitinised oval plate (figs. 2 and 3, op.). The anus is situated near the rear edge of the plate (fig. 2). A pair of little oval *paraprocts* (parp.) cover the anal orifice (an.). The *aedeagus* (aed.) is withdrawn into the cavity beneath the oval plate when not in use. It is a soft organ pointing forwards, the base of it being surrounded by two lateral bandlike sclerites (2) and a little ventral, **V**-formed sclerite (2). The opening of the **V**-formed sclerite points posteriorly. In the rear wall of the cavity, above the aedeagus, a little shield-formed sclerite (3) is seen. From the top of the shield a thin-forked arm follows the roof of the cavity. Laterally of the aedeagus a pair of oblong quadrangular inner forceps (i.f.) are to be seen. Their angles are drawn out in sharp points. They are about twice as long as they are high. Their upper angle at the rear end articulates to a sharp point on the edge of the oval plate. A very thin, chitinous arch (4) connects the upper angle of the front part of the two forceps. From the middle of the arch a very fine arm pointing anteriorly follows the roof of the cavity (5) and because of the folded roof of the cavity, it is bent like the letter **S**.

When coitus takes place, the aedeagus is pushed out of the cavity. During this action, the shield-formed plate is drawn downwards and forwards and rests in the dorsal wall of the aedeagus. The forceps turn round their articulation to the oval plate until standing perpendicularly on their ends. The top of the arch is drawn backwards so that the arch takes a horizontal position.

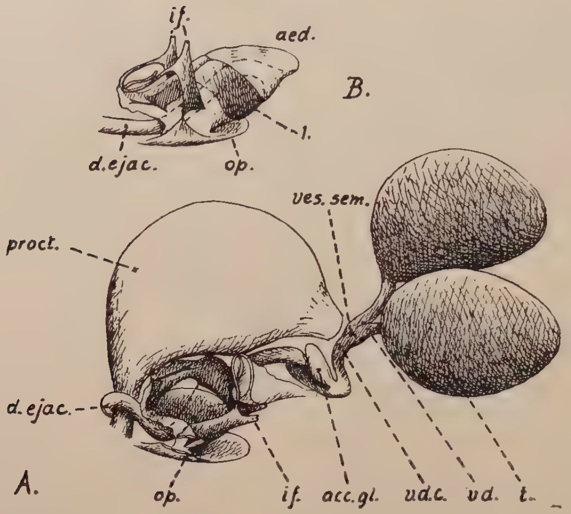

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FIG. 3.—*S. unicornis* Czerny, ♂. *A*, reproductive system; *B*, sclerotised parts.

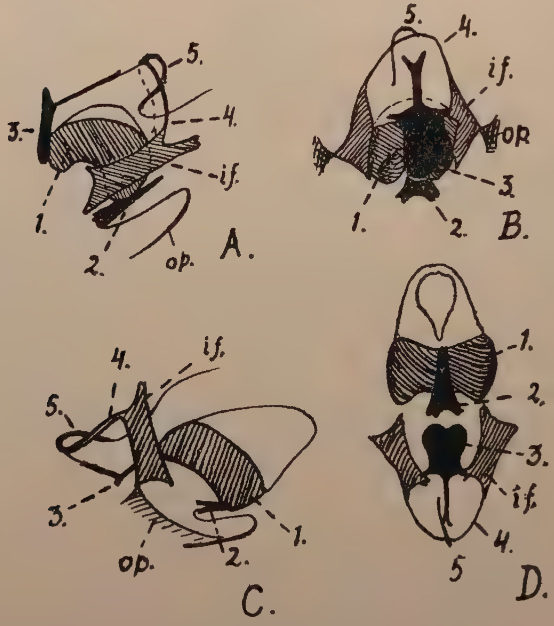

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FIG. 4.—The sclerites of the hypopygium. *A*, seen from the right; *B*, seen in dorsal aspect; *C*, seen from the right, and *D*, seen in ventral aspect. *A* and *B* in resting position.

The *testes* (figs. 3, t. and 5) are a pair of orange-coloured, ovoid bodies situated on each side of the intestine in the abdomen. Their rear end is broadest. A slender tube goes out from the caudo-median end of each of the testes. The tubes are the *vasa deferentia* (v.d.). The two vasa deferentia unite into an unpaired *ductus ejaculatorius* (d. ejac.). A pair of *sac-like glands* (acc. gl.) open into the front part of the ductus ejaculatorius. The ductus ejaculatorius opens with its rear end on the terminal end of the copulatory organ: the *aedeagus* (aed.).

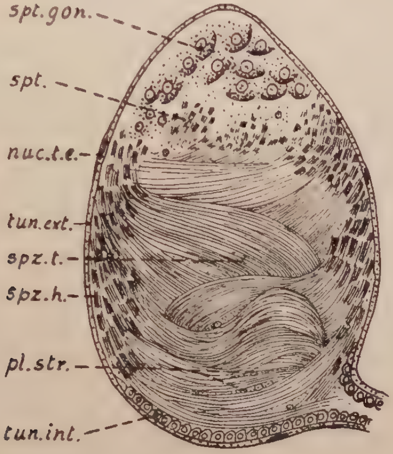

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FIG. 5.—*S. unicornis* Czerny. Testis.

The outer surface of the testes is covered by a thin epithelial layer. This layer is the *tunica externa* (tun. ext.). It consists of flat, strongly pigmented cells, the nuclei (nuc. t.e.) of which are flattened. In the rear end of the testes another epithelial, *tunica interna* (tun. int.), layer is seen underneath the tunica externa. It consists of large cubical cells with large clear nuclei. In the front part the testes contain groups of cells. These cells are the *spermatogonia* (spt. gon.). Their nuclei are large and clear and their plasma is filled with a substance which stains strongly in haematoxylin. They seem to have lost their ability to form new *spermatocytes*. It must be supposed that they have a function as nurse cells for the *spermatids* and the *spermatozoa*. No *apical cell* is seen. Most of the space of the lumen of the testes is filled with *spermatozoa* (spz. h., spz. t.) and *spermatids* (spt.). They lie in bunches corresponding to the groups of spermatocysts in an earlier stage. These bunches of spermatozoa and spermatids are surrounded by *strands of plasma* (pl. str.) belonging to cells supposed to be derivates of spermatocyst cells (*Friele*, 1930). The spermatozoa have each a long slender head (spz. h.) and a tail (spz. t.) that, so far as I can see, is longer than the whole testes. The pigmented tunica externa, as well as the tunica interna, continue in the *vasa deferentia* (v.d.) fuse, and widen to a small *vesicula seminalis* (ves. sem.). From the vesicula seminalis a short, slender, pigmented tube continues posteriorly. This tube must be of the same origin as the vasa deferentia and the vesicula seminalis, and therefore I call it the "*vas deferens communis*" (v.d.c.). *Keuchenius* (1913) has described a similar unpaired vas deferens in SYRPHIDAE. Backwards the vas deferens communis continues in a long *ductus ejaculatorius*

(d. ejac.). The wall of the ductus ejaculatorius is much thicker than that of the vas deferens. On its outer surface it is covered by a very thin epithelial layer, the nuclei of which are very small and dark. The inner surface is covered by an epithelial layer of rather large cells. Between these two epithelial layers is seen a thick layer of circular muscle fibres.

Two little *sac-formed glands* (acc. gl.) open into the anterior end of the ductus ejaculatorius. Their walls consist of an outer very thin epithelial layer and an inner epithelial layer of large, low cells.

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AN ARTIFICIALLY PRODUCED MULTIPLE MIXED COLONY OF ANTS (HYM.)

By B. D. W. Morley, F.Z.S., F.R.E.S.

In an earlier note (1939, *Ent. Rec.* **51** : 60) I recorded certain observations on a mixed colony of *Acanthomyops* (*Dendrolasius*) *fuliginosus* (Latr.) and *Acanthomyops* (*Chthonolasius*) *mixtus* (Nyl.) and also referred to an experimental introduction of some ☿☿ of the common black ant (*Acanthomyops* (*Donisthorpea*) *niger* (L.)) into the same nest. In that case some *niger* ☿☿ were introduced into a jar, in which some *fuliginosus* ☿☿ had previously been placed and later taken out, and left there for half an hour. The *niger* were then introduced into the mixed *fuliginosus–mixtus* colony. The object being to endeavour to pass on something of the extremely strong odour of the *fuliginosus* to the *niger* ☿☿ and thus facilitate the formation of an artificial mixed colony. This experiment was hardly a success; the *niger* habit of " saluting " (Donisthorpe, 1927, *Brit. Ants* : 208) seems to annoy the other ants concerned, though Donisthorpe (1927, *Brit. Ants* : 225) records a mixed *fuliginosus–umbratus–niger* colony which he produced in one of his observation nests.

It seemed to me that ☿☿ of several species might well be induced to live together peaceably if the species concerned were so chosen that their nest odours would not be entirely strange one to another and if this differentiation of nest odours was made less noticeable by a background of strong *fuliginosus* odour. Now *Formica fusca* L. and *Formica rufa* L. are not strangers, neither is *rufa* and *Leptothorax acervorum* (Fab.), nor *rufa* and *fuliginosus*. Thus ☿☿ of these four species might well live peaceably together.

I therefore introduced some *fuliginosus* into an observation nest with some *Leptothorax acervorum*, followed by a few *rufa* ☿☿ and next day some *fusca* ☿☿. The *fuliginosus* outnumbered the total number of all the other three species. These four species, after being a bit quarrelsome at first, soon settled down perfectly happily.

I then formed another similar mixed colony containing, as did the other one, a base of *fuliginosus*, but having *Acanthomyops* (*Chthonolasius*) *mixtus* (Nyl.), *Myrmica ruginodis* Nyl., and *M. laevinodis* Nyl., instead of *rufa*, *fusca* and *acervorum*. Once again it should be noted that the species concerned were chosen so that they would not be entirely strange to one another since they may meet in their natural habitat, and even intermingle. This colony also settled down peaceably. These two colonies were kept separate for a fortnight, and then put into one nest. Rather contrary to my expectations, but in accordance with my hopes, they mixed and settled down all right. Here then was a nest containing eight different species living together happily, though normally there would have been a battle royal; this result being achieved by means, apparently, of the *fuliginosus* with their strong nest odour, and careful mixing. Later some ☿☿ of the rather cowardly *Acanthomyops* (*Chthonolasius*) *flavus* (Fab.) were also put in, and settled down all right.

PROC. R. ENT. SOC. LOND. (A) 15. PTS. 10–12. (DECEMBER 1940.)

It is worthy of mention that only a few *rufa* ☿☿ can be placed in a plaster observation nest, as on hot days they tend to get excited and squirt acid, which, if there are many *rufa*, drops off the glass cover, killing both them and the other ants in the nest.

Mixed colonies were obtained artificially by Miss Fielde by means of (*a*) mixing the species in the pupal stage, and letting them hatch out as a mixed colony, and (*b*) by amputating the antennae of the ants concerned, as was pointed out by Donisthorpe (1940, *Proc. R. ent. Soc. Lond.* (C) **5** : 23) when I exhibited the colony to the Royal Entomological Society, but I believe that this is the first time that success has been achieved with adult, and uninjured, ants.

Book Notice.

Symposium on Fifty years of Entomological Progress. *J. econ. Ent.* **33** : 8–65. 1940.

This symposium consists of 5 papers by C. L. Marlatt, L. Caesar, C. L. Metcalf, E. O. Essig, and S. A. Rohwer, each of whom writes of the progress made in one of the 5 decades from 1889 to 1939. The papers were read at a joint session of the American Association of Economic Entomologists and the Entomological Society of America, and it is natural that the main concern of the authors is the development of Entomology in the American continent. The American Association of Economic Entomologists was formed at Toronto in 1889 and its official publication is the *Journal of Economic Entomology*, of which 33 volumes have been published.

Book Notice.

The Problems of Insect Study. By P. Knight. 2nd Edition. 4to. Ann Arbor (Edwards Bros.), 1939. pp. vii + 132, 22 pls., 31 figs. Price $2.50.

This book is lithoprinted in double columns and comprises 6 chapters: Chapter 1, The Insect problem; 2, man surveys the damage; 3, man counts the gains; 4, man appraises a competitor; 5, man classifies the Hexapods; 6, tentative solutions. Two appendices deal with the literature of Entomology and the common and scientific names of insects.

" The selection of the subject matter . . . has developed primarily out of questions of students and the introductory course in Entomology at the University of Maryland during the past 15 years."

" The final outcome was a course dealing with the science and problems of Entomology rather than a course about specific insects . . ."

The result is this book which gives a great deal of information of a popular interest which is not easily found elsewhere.

AN OUTLINE OF THE HABITS OF THE WATER-BEETLE, *NOTERUS CAPRICORNIS* HERBST (COLEOPT.)

By Frank Balfour-Browne, M.A., F.R.S.E., F.L.S., F.Z.S., F.R.E.S., and
John Balfour-Browne, M.A., F.Z.S., F.R.E.S.

This is a joint paper because the honours as to the discoveries connected with the habits of the beetle are divided. The junior author first discovered the larva and how to obtain it in quantity, while the senior author discovered the pupa. It is now possible to outline the life-cycle of this species although, so far, all the details have not been directly observed.

Oviposition apparently takes place during the summer. This is deduced from the fact that, in various places observed, the imago is in abundance in the spring and becomes scarce about June, from which we conclude that the ovipositing females and their males are dying out about that time. The imagines are abundant again by the beginning of August, many specimens being soft, indicating the emergence of the next generation, but at that time small and large larvae and pupae are also obtainable, so that the breeding period presumably extends throughout the summer and early autumn.

The imagines, kept in an aquarium, spend a large part of their time burrowing in the soil and as the larvae live among the roots of water-plants in twelve to eighteen or more inches of water, it seems reasonable to assume that the eggs are laid where the larvae are found. From the nature of the ovipositor, it seems probable that the eggs are laid on, not in, the roots or are deposited on or in the mud, the larvae themselves in the latter case burrowing to their food. From watching the larvae, we have seen the rapidity with which they move through the soil at the bottom of the observation dishes, a quality which makes it difficult to discover them on the collecting sheet. The larvae are a pale yellow in colour and are found by pulling up plants of *Iris*, *Alisma plantago*, *Sparganium ramosum*, etc., amongst the roots of which they are common. Occasionally, an odd specimen floats to the surface as the plant is pulled up and this was how our first example was found. The insect was caught in the surface film and the net happened to catch it before it could release itself. But this searching of the water surface after pulling up the plant provides a poor harvest and the method the junior author quickly devised was to pull up the plant and immediately to get the net underneath it and then to wash the root thoroughly within the net. After considerable washing, the contents of the net were emptied on to the collecting sheet so spread as to leave a slight dip in the middle and some water was added, if necessary, so as to make a shallow muddy pool. This pool was then stirred up with the fingers and the larvae floated to the surface, where they were caught in the surface film and collected. Even so, perhaps only a single larva appeared but by repeating the stirring at intervals quite a number of specimens were taken from a single root. The senior author must confess that he was much less successful at this process, so that the personal element comes into play here as in all collecting. Once the method of finding the larvae had been discovered, it was easy to find them almost anywhere we searched for them.

PROC. R. ENT. SOC. LOND. (A) 15. PTS. 10–12. (DECEMBER 1940.)

A number of specimens was brought home and kept alive in flat glass dishes in which a small amount of soil had been placed and they at once exhibited the method of renewing their air-supply described by Wesenberg-Lund (1912), bringing the apex of the abdomen to the surface like any Colymbetine or Dytiscine larva. But it is obvious that larvae living in the mud in a foot or more of water cannot return to the surface at intervals in order to renew their air-supply, so that they must have some other method in deep water. It was noticed that the larvae in the flat dishes frequently placed the apex of the abdomen against pieces of root placed in the dish, but the attempts at piercing seemed very feeble.[1]

That the larva of *Noterus* does thus obtain its air-supply was suggested by G. W. Müller (1922) and it seems probable from the form of the apex of the abdomen. On the other hand, there is the possibility that the larva can obtain its air from the water, as do those of the Hydroporines, and in this connection it is interesting to note that the junior author has found that if these Hydroporines are kept in shallow water, they use the atmospheric air by bringing the apex of the abdomen to the surface. We mention this merely as a possibility although, from the habits in connection with pupation, it is obvious that the larva taps the plant root when it constructs its cocoon on the root, and therefore it almost certainly does the same during its feeding period. The cocoon is full of air so that when a plant upon the roots of which cocoons are attached is pulled up and vigorously shaken the cocoons float to the surface. I have seen these cocoons times innumerable but have always passed them over as seeds and it was only because we had found the habits of the larva that I opened some of them and discovered what they contained. There can be little doubt but that many entomologists have seen these cocoons and, doubtless, they have been seen by botanists and passed over as unimportant.

To those who know the life-history of the Chrysomelid beetles of the genus *Donacia* the similarity between it and that of *Noterus* will at once occur. MacGillivray described the life-history of these beetles in 1903. The larvae live in the mud on the roots of water-plants and possess two " caudal setae " which pierce the root tissues and, having the spiracular opening at the base, the air in the plant reaches the tracheal system of the larva. The full-grown larva forms an oval blunt-ended cocoon, which is at first transparent and is produced from a secretion from the larva. This cocoon is attached along one side to the root and the larva bites one or more holes in the root tissue to make contact with the air spaces of the plant.

MacGillivray stated (p. 312) that " if the place from which a cocoon has been removed is examined, there are found two slits near one end " in addition to the bitten hole, and points out that these slits are made by the caudal setae. In the two British species I have investigated, the slits are quite easily recognised beneath one end of the cocoon, but as *Noterus* builds its cocoon with its end on the root and bites a hole, like *Donacia,* for the air-supply, this hole occupies the whole surface of contact and the small puncture which the insertion of the apex of the abdomen would make is not recognisable.

MacGillivray did not explain how the cocoon becomes filled with air, merely stating that the larva entirely surrounds itself while spinning the cocoon " by a quantity of air sufficient to fill the vacant space in the cocoon" (p. 313). The only possible explanation appears to be that the lacerated root tissues give off air, which is caught in the cocoon as it is being constructed and is sealed within it when the larva closes the distal end. We have to thank Professor F. T. Brooks for confirming this view of the action of the root. Once the cocoon is filled with air, exchange of gases will take place between it and the root as the larva or pupa exhausts the oxygen. It is to be noted that the cocoons of *Noterus*, opened while the larva is still within, are already filled with air and they reveal the larva with the apex of the abdomen at the root end, the larva lying curved almost double. The pupa invariably has the larval skin lying in a strong curve on its ventral side (pl. 1, fig. 6), its own abdomen being towards the root. The pupa, however, has no spine or piercing apparatus and is, in this, similar to that of *Donacia*.

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[1] The larvae of *Donacia*, which also obtain their air from the roots of water-plants, were stated by Schmidt-Schwedt to insert their caudal spines into the tissue of the root when kept in the dark but to withdraw them immediately when brought into the light. (From MacGillivray, 1903 : 307.)

It is interesting that two groups of beetles so widely separated as the Noterines and the Donacias should have developed such similar habits in the larval and pupal stages. There seems to be no doubt but that the *Donacia* larva is entirely vegetarian, and Wesenberg-Lund (p. 56) assumed from the form of the mandibles that the *Noterus* larva is the same. In our observations on the specimens in our dishes, they occasionally worked their mandibles upon the surface of the roots without, however, appearing to get anything off. They readily attacked dead *Chironomus* larvae and also dead individuals of their own kind but after an apparently ravenous attack lasting a very short time, the prey was left and not again attacked. As the larvae failed to live more than a few days in our dishes, we have not so far discovered their normal food, although it is possible to make deductions from a comparison of the mandible with that of *Donacia* (see p. 109).

The Larva (pl. 1, figs. 1 and 2).

A description of the larva may be useful as there has not previously been one in English and the accounts given by Meinert (1901) and by Wesenberg-Lund (1912) are not entirely accurate. Müller's (1922) description is somewhat vague and the one figure he gives of the apical abdominal segment is very sketchy. The colour, as already mentioned, is pale yellow, the underside of the abdomen white. The full-grown larva is about 9 mm. long and is narrow and resembles an Elaterid larva in general appearance (pl. 1, figs. 1 and 2). As Müller stated that the larvae he found were 6 mm. long (" apparently full grown but rather retracted "), it is possible that he had specimens of *N. clavicornis* as he suggested.

The head and thoracic segments are completely encircled with strong chitin, but all the abdominal segments have the ventral surface soft. Each abdominal segment is capable of being telescoped into the one in front of it and the eighth segment can be almost completely withdrawn into the seventh (see fig. 1, B).

There are eight pairs of abdominal spiracles in the third stage larva, one to seven being easily seen as small circular pits in the chitin at the sides of each segment, rather nearer the front than the back of the segment. The eighth pair lie side by side at the extreme apex of the segment, immediately beneath the chitinous point. These two spiracles communicate each with a " vestibule " in the segment into which the lateral tracheal trunk of its own side enters (see fig. 1, B). These trunks are apparently similar to those of other insects but the taenidial threads, which give the characteristic transverse markings seen from the side, are only faintly visible. There do not appear to be any thoracic spiracles, but the tracheal branches, leading to where the mesothoracic spiracles would be, can be seen through the chitin.

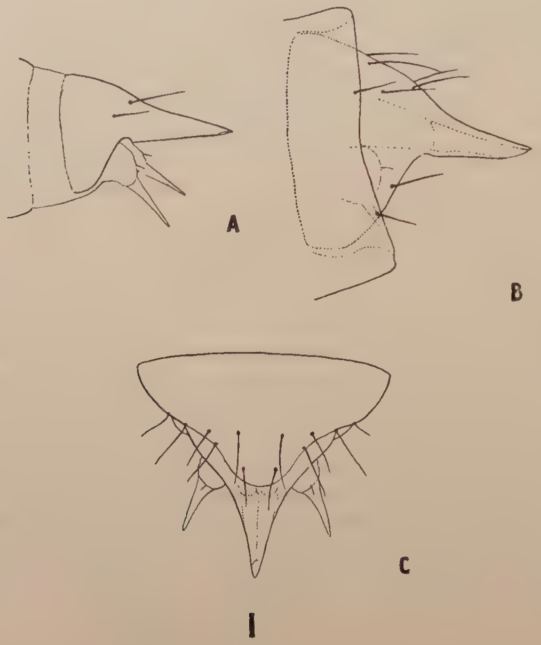

Fig. 1.—The last (eighth) abdominal segment of the larva of *Noterus capricornis* Herbst: (A) in a young larva, 3·5 mm. long; (B) in a full-grown larva, 9 mm. long, both seen from the side. In (A) the cerci are exserted and in (B), segment 8 is withdrawn into segment 7 and the cerci are packed away; (C) shows the dorsal view of the segment in a full-grown larva. Both (B) and (C) are from specimens boiled in potash and flattened on the slide.

The eighth abdominal segment (fig. 1) bears below the chitinous point a pair of small cerci, the bases of which are capable of being expanded or contracted so that the cerci may at one time project distinctly from the segment while at another they are only just visible. The anus lies below and between the bases of these cerci.

The Head Appendages.

The head bears the usual appendages. The antennae are 4-segmented and simple (fig. 3, A). The labrum (fig. 2, A) has a peculiar central part in which the epipharynx appears to break through to the upper surface. The maxillae (fig. 2, B) consist of a small basal cardo bearing a large stipes upon which are the 4-segmented palp and the subgalea carrying the galea. The basal segment of the palp appears to be part of the main structure of the maxilla but the palp is probably similar to that of other Dytiscids. Meinert (1901, pl. VI, fig. 155) figures a single hair on the penultimate segment of the palp but there appear to be single hairs on the outer side of each of the three basal segments and also two hairs, side by side, in the membrane between the stipes and the basal segment of the palp, on the outer side.

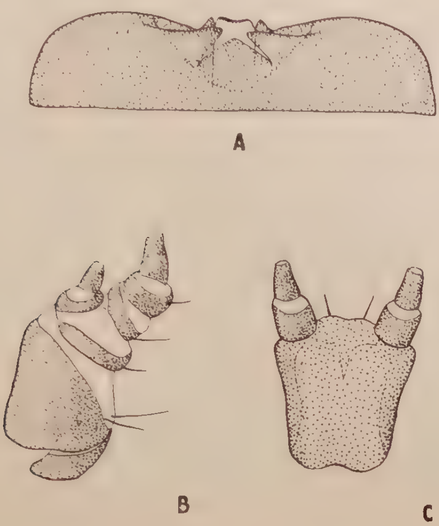

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FIG. 2.—(A) labrum; (B) maxilla; (C) labium of larva of *Noterus capricornis* Herbst.

The labium (fig. 2, C) is simple and bears two 2-segmented palps and between them are two simple hairs. Meinert (pl. VI, fig. 156) figures each of these hairs as double but I could only agree with him by employing excessive magnification which, I believe, produced distortion.

The mandibles (fig. 3, B) are not quite as figured by Meinert (figs. 153, 154) or by Wesenberg-Lund (1912, pl. III, fig. 21b). From our figure it will be seen that the upper half is grooved down the inner face and toothed on both sides of the groove. This groove forms a pocket at its lower end, and about half-way down the inner face there projects a large pointed tooth, behind which is the pocket just referred to. Below this tooth is an edge armed with a few minute spines or teeth.

Snodgrass (1935 : 286) states that " with phytophagous species there is generally a well-marked differentiation in each mandible between a distal incisor lobe with cutting edge and a basal molar lobe provided with an irregular masticatory surface. In the predacious species, however, the grasping function of the jaws is more important than that of chewing, and in such species the mandibles are usually simple biting organs with strong incisor points which may be notched or toothed but in which effective molar surfaces are generally absent."

According to this definition, the mandibles should probably be regarded as of the predacious type but a comparison of them with those of *Donacia* (fig. 3, C) shows that there are similarities and that the *Noterus* mandible might be regarded as a modification of the phytophagous type. The apical point of the mandible of *Donacia* is slightly hollowed out on its ventral side, and the inner face, at the base, although not a true molar surface, bulges slightly. In

Noterus, the secondary tooth is much lower down and the molar process is absent. The general form of the mandible, however, suggests that it would still serve as an efficient organ for biting the root tissues, as it certainly does

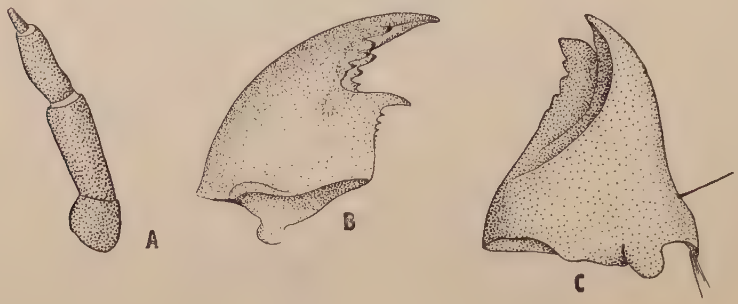

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Fig. 3.—(A) antenna; (B) left mandible of the larva of *Noterus capricornis* Herbst; (C) ventral view of left mandible of *Donacia* sp. larva.

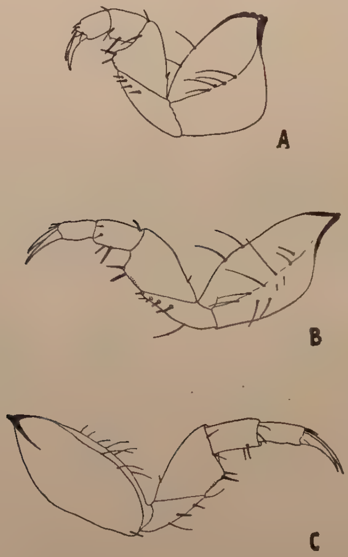

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Fig. 4.—(A) right fore leg, anterior side; (B) right mid leg, anterior side; (C) right posterior leg, posterior side, of the larva of *Noterus capricornis* Herbst.

when arranging the air-supply for the cocoon, and that it would be suitable also for chewing animal organisms, as we observed it doing. Possibly, therefore, the larva flourishes on a mixed diet.

The Legs.

The descriptions of the legs given by the three authors referred to are incomplete and the figures given by Meinert and by Wesenberg-Lund are not quite accurate. The coxa is large and in the black chitinous structure at its base in each leg there are three minute circles arranged in a triangle which appear to be punctures going through the chitin. In some other larvae, *e.g.* some Colymbetines, similar spots occur but not, apparently, in groups of three.

The chaetotaxy of all legs is practically the same (fig. 4). The coxa has, on its upper or outer face, a flat area against which the closely united trochanter and femur lie when the leg is drawn up against the body. The posterior margin of this flat area carries two rather long fine hairs or spines, while the anterior margin, in the fore leg, carries four and in the mid and hind legs additional spines, about six along the margin and some more in the immediate neighbourhood.

The anterior face of the trochanter has always four short thick spines and the posterior face has two. The femur has a single small spur on its rounded dorsal side and on its ventral side at the distal end are a pair of strong spines. The tarsus consists of one segment and bears two freely movable claws, as in other Dytiscids. These claws are slightly different in length, the anterior being a little longer than the posterior. The figures show this difference and the whole of the chaetotaxy.

The Cocoon.

The full-grown larva constructs a cocoon of small pieces of vegetable material mixed with mud-particles on the roots of various kinds of plants growing in the water (pl. 1, figs. 3, 4 and 5). The cocoon is oval in shape, about 4·7 mm. long and is built end on to the root. It is strongly lined with a material, presumably produced by a larval secretion, and this lining covers the hole bitten in the root, so that all the inner surface of the cocoon is smooth.

We do not know how long the cocoon persists but it is probably not more than a few weeks and in this *Noterus* differs from *Donacia* in which the cocoon stage lasts " ten months or more " and " the pupa transforms to the beetle long before it is time for it to emerge." The imago of *Noterus* emerges in the same season in which the larva forms the cocoon by biting a more or less circular piece from the distal end.

The pupa (pl. 1, fig. 6) is white and of the usual coleopterous type.

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EXPLANATION OF PLATE 1.

FIG. 1. *Noterus capricornis* Herbst. The larva seen from the side. The photograph was taken from a specimen cleared with potash and mounted in balsam so that the spiracles on both sides of some of the abdominal segments are visible.

2. *Noterus capricornis* Herbst. Ventral view of the larva. The "soft" sterna of the abdominal segments are visible.
3. *Noterus capricornis* Herbst. Pupal cocoons on the roots of *Sparganium ramosum.* The circular exit hole made by the imago is visible in several of them.
4. Pupal cocoons of *N. capricornis.*
5. Pupal cocoons attached to a root.
6. Pupae of *N. capricornis* with the larval skin in its normal position.

BOOK NOTICE.

Sawflies of the Berkhamsted District, with a list of the Sawflies of Hertfordshire and Buckinghamshire, and a survey of the British Species (Hymenoptera Symphyta). By R. B. BENSON. *Trans. Herts nat. Hist. Soc.* **21 :** 177–231, 1940. Price 5*s.*

This work is the result of collecting carried out during the last 18 years by the author and the few published records of species taken in the area dealt with.

There is a very long introduction followed by the list of species to the number of 313. Four hundred and thirty-six species have been recorded from Britain. For each species the locality is given and some details of its frequency of occurrence and time of appearance.

BOOK NOTICE.

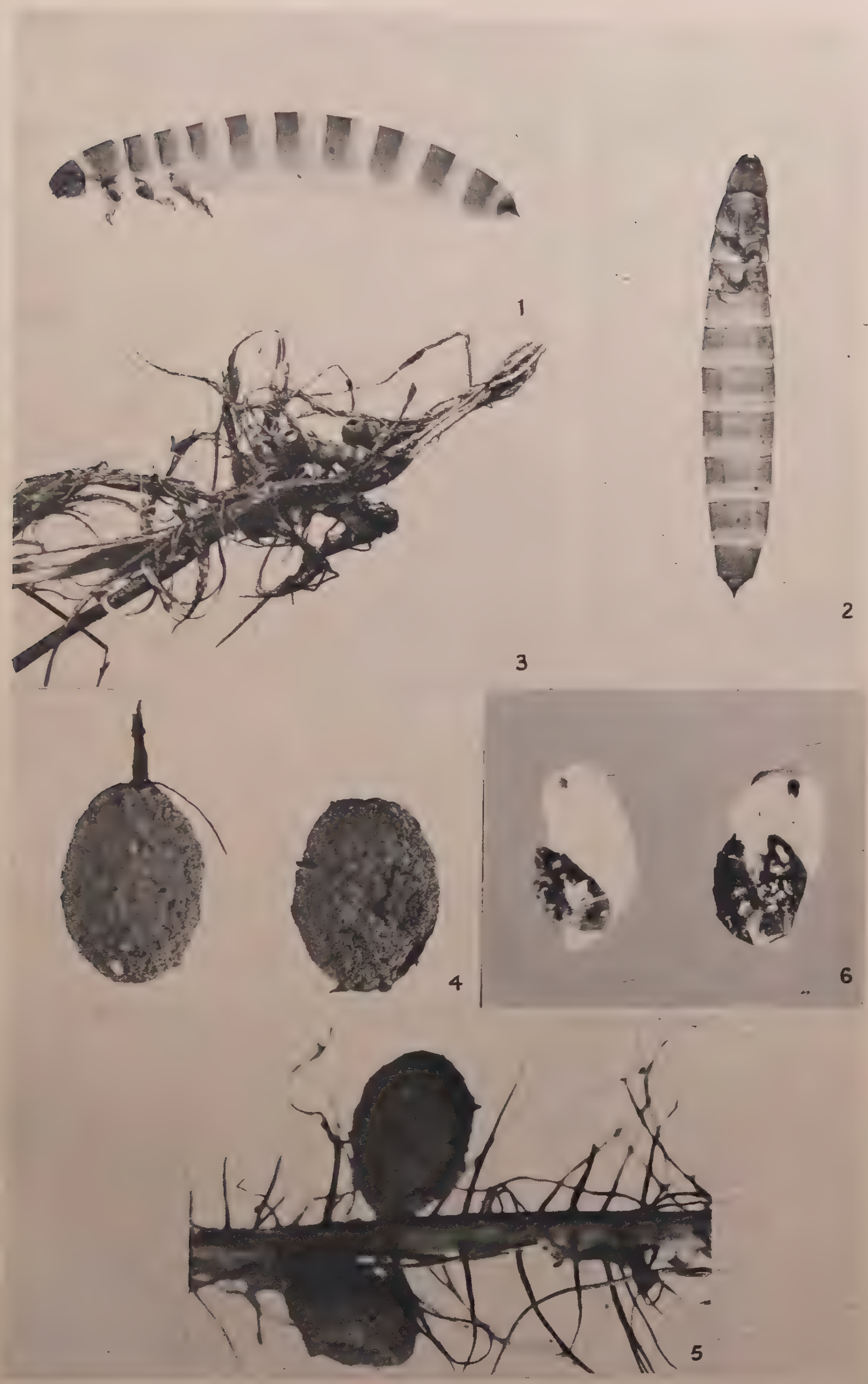
Insect Pests. By W. C. HARVEY and H. HILL. 8vo. London (Lewis), 1940. Price 10*s.* 6*d.* pp. ix + 292, 23 figs.

The authors of this book are a medical officer of health and a sanitary inspector to a local authority.

The book is in two parts : the first relating to insect pests and the second to principles and practice of disinfestation. There are two appendices giving samples of forms and propaganda leaflets suitable for use by a local authority.

There is a special chapter devoted to each of the following : the bedbug, the flea, and the louse and one chapter to the cockroach, cricket, silver fish, ant, itch mite, psocids, earwig, woodlice and the house fly.

The second part deals with building construction, fumigants, control and educational measures, legislation, and disinfestation of foodstuffs and ships.



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F. & J. Balfour-Browne. Habits of **Noterus capricornis.**

A FILTER-FEEDING MECHANISM IN A LARVA OF THE CHIRONOMIDAE (DIPTERA: NEMATOCERA)

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Communicated by Dr. W. H. Thorpe, F.R.E.S.

This paper deals with the method of feeding observed by me in the larva of the Chironomid *Glyptotendipes glaucus* (Mg.). I have also compared the behaviour of this Chironomid larva with what I could learn from the literature concerning comparable habits in the larvae of other species of Chironomids.

The larva of *G. glaucus* is found very commonly in the submerged leaf bases of the reed mace *Typha latifolia* L.; more particularly those which are dead and have already begun to decay. However, it is not restricted to this habitat, for I have found the larvae making their galleries in pieces of rotting submerged timber, and in the cavity of a drifting stem of *Phragmites*.

The structure of the larva itself calls for little comment. Its general appearance is shown in fig. 1, where it will be seen that it has the typical form of a Chironomid larva without any ventral so-called gill filaments, but with the usual anterior and posterior pairs of appendages armed with hooks. The arrangement of the mouth-parts and details of the antennae, mandibles and labium are shown in fig. 2. The larva attains a length of about 14 mm., and is bright red in colour owing to the haemoglobin present in the body fluid.

Some details of the pupa are given in fig. 3. The most characteristic features are the dorsal spatula-like projections on the 2nd, 3rd, 4th, 5th and 6th abdominal segments which coincide with dorsal depressions in the abdominal segments of the adult fly. The typical members of the genus *Glyptotendipes* show this character. Another character useful in separating different pupae is the form of the spines on the postero-lateral angle of the penultimate segment; the form of which is shown for *G. glaucus* in fig. 3, b and c.

The larval and pupal characters of this insect are very similar to those described by Gripekoven (1914) for the larvae and pupae of *Tendipes sparganii* Kieff., *T. ripicola* Kieff., *T. fossicola* Kieff., and *T. stagnicola* Kieff. The structure of the larva is also very similar to that described for *Tendipes gripekoveni* Kieff., although my larva is rather too small for *gripekoveni*. Both Edwards (1929) and Goetghebuer (1937) give *Glyptotendipes* (= *Tendipes*) *gripekoveni* as a distinct species judged from the adult, while the species which Edwards refers to as *Glyptotendipes glaucus* is designated *G. pallens* by Goetghebuer. The latter authority includes *ripicola*, *stagnicola* and *fossicola* under the one species *Glyptotendipes pallens* (Mg.).

The Feeding Mechanism.

The larva eats out a tube in the leaf bases of *Typha*, making use of the elongated air cavities which fill the space between the two surfaces of the leaf. The larva starts by eating a round hole and crawling into one of the air spaces;

then it bites through the cross-walls which separate the air spaces until the gallery is long enough. The inside of the tube is lined with a layer of silk spun from the salivary glands; at each end the tube opens by a distinct hole eaten through the cuticle of the leaf; and the gallery beyond this point is closed either by a silk wall or by a layer of silk applied to one of the cross-walls of the air spaces. The arrangement of the tube is shown in fig. 1.

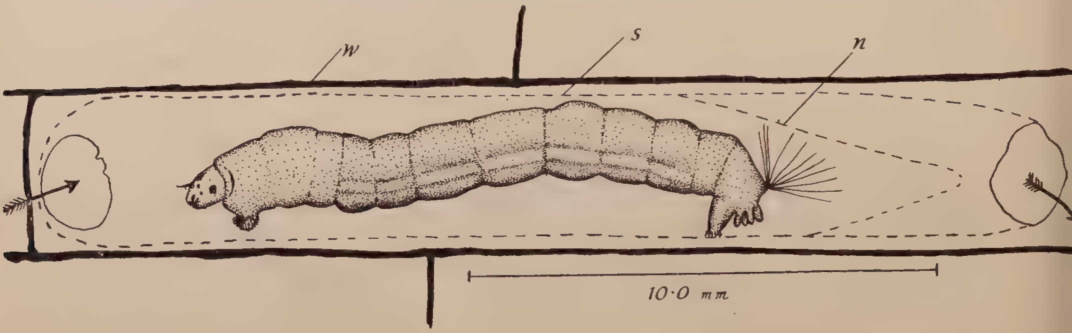

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FIG. 1.—Larva of *Glyptotendipes glaucus* (Mg.) in its tube in a leaf of *Typha*. The outer wall of the tube is imagined to be transparent. Lettering—n, net; s, wall of tube; w, wall of air space. The arrows show the direction of the current.

Within its tube the larva anchors itself by the fore and hind limbs to the lining of the wall and sends waves of movement down its body from head to tail: the plane of vibration of the body being the same as that of the paper in fig. 1. This action has the effect of driving a stream of water through the tube; the particles carried in this current are caught; and form the chief food of the larva. The mechanism of catching the suspended matter is as follows. The larva spins across its tube a web which is shaped exactly like a plankton net with its mouth lying towards the anterior end of the tube (see fig. 1). The actual spinning of this net is difficult to follow because it is a very fine structure which is not distinctly visible until it has entangled a number of particles. The movements which accompany the weaving of the net are, however, very characteristic. The larva presses its mouth against a point on the wall near the end of the tube and then moves sharply backwards (I interpret this as the action of fixing and drawing out the silk); then it moves slowly forwards, alternately contracting and expanding its fore legs (presumably pressing the silk into position). These actions are repeated in several different planes (always starting from the same point of attachment) until the net is complete, when the larva turns round in its tube. Owing to the narrowness of the latter, the larva has to bend quite double to get round and often spends some time cleaning the ventral side of its body during the process of turning. Immediately the larva has reached its new position, it starts to send waves down its body from head to tail and soon the particles driven into the net render the latter clearly visible. This is the position of the larva shown in fig. 1. The pumping goes on for a few minutes and then the larva turns again in its tube, but now it seizes the open end of the net in its jaws and twists the net by rolling its body round its long axis, first in one direction and then in the other, devouring the net the whole time. Once the mass of silk and its contained particles have been eaten, the larva starts to spin another net and the process is repeated.

The fine structure of the tube and net is best made out by staining a portion with borax carmine. A piece of the wall of the tube appears as a mass of fine wavy fibres less than 2 μ in thickness running in all directions. The net is very similar, only the fibres are not nearly as closely placed, and spaces varying from 5 to 40 μ are left between them.

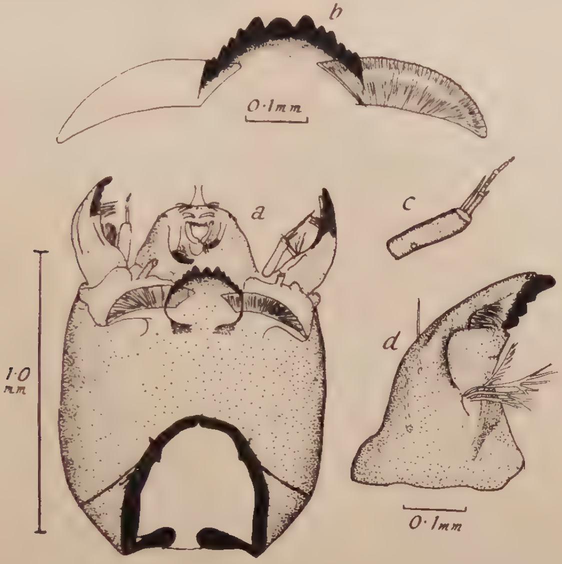

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FIG. 2.—Larva of *Glyptotendipes glaucus* (Mg.). a. head in ventral view; b. labium; c. antenna; d. mandible.

It is interesting to watch the various ways in which the rhythm of spinning–pumping–eating may be modified. If one measures the number of beats made per minute while the larva is pumping and the duration of the period of pumping (or in other words, the interval between spinning and eating the net), one finds that the more rapid the strokes of the body, the shorter is the interval between spinning and eating the net. Below are some rates taken for the same larva at different times. The rate of beating was judged by taking the rate at intervals of one minute with a stop-watch, and then finding the average for the whole period. There was generally a slowing of the rate of beating towards the end of any one period. This may be due to the increased resistance of the net as it becomes clogged with particles.

Period of pumping	Rate of beating
45 minutes	44 per minute
16¾ ,,	66 ,,
14½ ,,	68 ,,
12 ,,	81 ,,
11¼ ,,	82 ,,
11 ,,	77 ,,
10 ,,	71 ,,
9 ,,	89 ,,
7 ,,	103 ,,
7 ,,	115 ,,
6 ,,	131 ,,

I have arranged the lengths of the periods of pumping in diminishing order; whence it will be seen that the rate of beating becomes, on the whole, more rapid, although there is no simple proportionality between the two. There are two rhythms in the feeding of this larva: there is the rapid beat of the body movements, and then superimposed on this is the slower rhythm of spinning, eating and turning round in the tube. Acceleration of one rhythm is accompanied by acceleration of the other.

Bright light and rise in temperature accelerate the rhythm. It is worth noting that transferring the larva from well-aerated water into water from which the air had been removed by evacuation caused no quickening of the pumping movements, although one cannot lay much stress on this observation in view of the low oxygen tensions that can be endured by haemoglobin-containing Chironomid larvae.

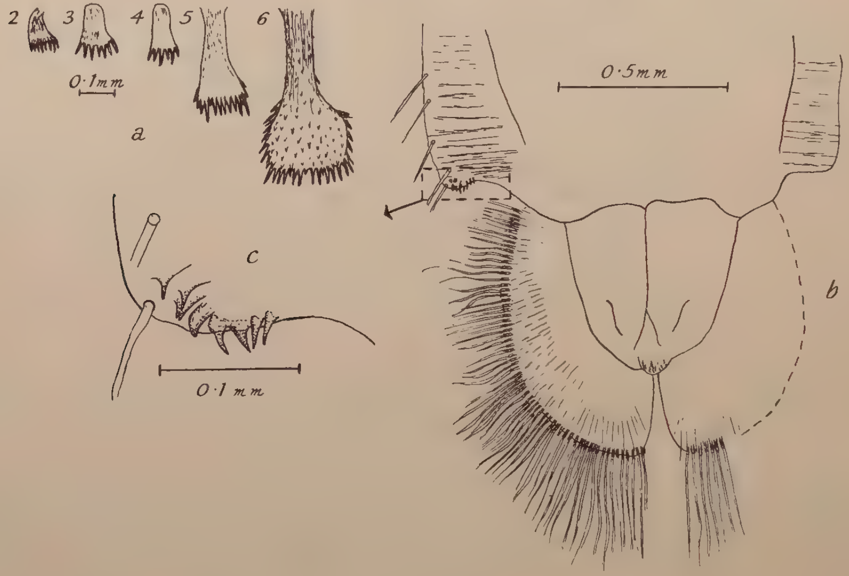

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Fig. 3.—Pupa of *Glyptotendipes glaucus* (Mg.). a. appendages on the 2nd, 3rd, 4th, 5th and 6th abdominal segments; b. end of abdomen showing inset the posterior angle of the penultimate segment; c. spines on penultimate segment.

It is natural to wonder whether there is any relationship between the condition of the net and the length of the interval before the larva turns round and eats it: whether, in fact, the larva can be said in any sense to eat the net when it is full. The absence of simple proportionality between the period of pumping and the rate of beating suggests that this is unlikely. Unfortunately it is not feasible to remove the net while the larva is pumping to see what effect this would have on its subsequent behaviour, because any tugging at the net stimulates the bunch of hairs at the end of the body, and causes the larva to stop pumping and either crawl out of its tube, or turn round and move towards the disturbance with its mandibles open. However, one can determine whether the period of pumping preceding the eating of a heavily charged net is shorter than that preceding the eating of a lightly charged one. It is very easy to add starch particles to the water which passes through the tube and thus add enormously to the amount of material in the net. Using a second larva the following figures were obtained :—

	Period of pumping	Rate of beating
With starch	5¼ minutes	104 per minute
	4¾ ,,	96 ,,
No starch	6¾ ,,	96 ,,
	5¼ ,,	105 ,,

A slight quickening was noticed in this case, but in no sense was it equivalent to the enormously different state of the net with clear water and starch suspension.

A number of observations were made on another species of net-making larva regarding its reaction to the blocking up of the tube. The larva of *Pentapedilum tritum* (Walk.) (see below) was very convenient on account of the small size of its tube. The anterior opening of the tube was blocked with a piece of silk taken from the tube of another larva, and at once the pumping became slow and laboured. I suspect that the larva becomes aware of the blockage by the increased resistance to the pumping movements. What usually happens is that the larva reverses the beat for a few strokes and then, if the blockage continues, it ultimately crawls to the anterior opening, eats a way past the obstruction and lines the new passage with silk. If the posterior opening were plugged, the larva still behaved in the same way and pushed its head through the perfectly free anterior opening several times : finally it turned round and ate the net, and, making a few pumping movements in this position, it encountered the resistance and then its response resulted in the clearing of the tube. The last observation shows how much the behaviour is adjusted to deal with those events which are normally encountered, but not with novel ones.

NATURE OF THE FOOD.

An examination of the net of a larva shows that the objects entangled consist of readily recognisable planktonic objects such as diatoms, algal cells and clumps of bacteria. Added to this are masses of material without any readily visible structure, but which arise in all probability from the decay of the plants in which the tube of the larva is made. It will be clear from what has been said of the feeding mechanism, that the larva exercises no selection on the objects which pass into the net.

SIMILAR NET-MAKING IN OTHER CHIRONOMID LARVAE.

I have tried to find how widespread this catching mechanism is among Chironomid larvae, and whether it is found in all those species which live in the stems of aquatic plants.

So far as I know the first careful account of a Chironomid larva living in the tissues of aquatic plants is due to Willem (1908). Under the name of *Chironomus sparganii* Kieff. he described a larva which, from the form of its mouth-parts, and from the possession of the characteristic dorsal spatula-like structures on the abdominal segments of the pupa, must be in the genus *Glyptotendipes* and perhaps is *G. glaucus* itself. He described the gallery made by the larva and stated that the food consists of diatoms, algae, etc., which get entangled in the silk walls of the tube and are scraped off by the larva. He does not describe the spinning and eating of the net. Gripekoven (1914) described over 30 species of Chironomid larvae which mine in aquatic plants, and among them some which have characters (*e.g.* the structures on the abdominal segments of the pupa) which place these larvae in the genus *Glyptotendipes*, but nowhere does he describe the peculiar feeding mechanism. He confirmed the account of Willem and suggested that the plankton is caught on the walls of the tube and that the bunch of hairs at the end of the body also acts as a trap.

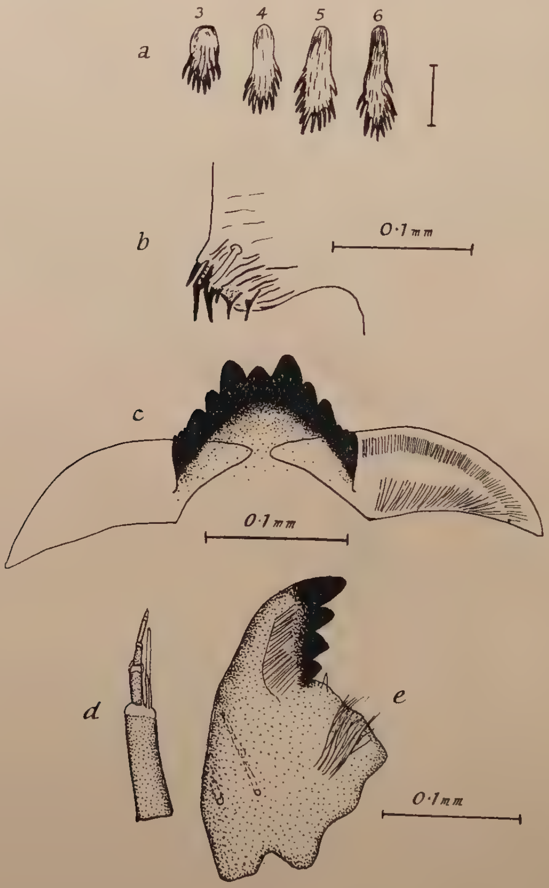

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Fig. 4.—*Glyptotendipes imbecillis* (Walk.) pupal and larval characters. a. structures on 3rd, 4th, 5th and 6th abdominal segments of pupa; b. spines on penultimate segment; c. labium of larva; d. antenna of larva; e. mandible of larva.

One might suppose that the net was a peculiarity of *Glyptotendipes glaucus*, but this is not so. I have found virtually identical behaviour in the larvae of *Pentapedilum tritum* (Walk.) and *Glyptotendipes imbecillis* (Walk.). The habits of these larvae are so similar to *Glyptotendipes glaucus* as not to require detailed description. They live in very similar habitats but their tubes are smaller in accordance with their size and the rate of their movements is more rapid under the same conditions. In both cases the larvae were reared and their species determined from the resulting adults. The general appearance of the larva of *G. imbecillis* is very similar to that of *G. glaucus* shown in fig. 1; but it is markedly smaller, not reaching more than 9 mm. in length, and the head seen in ventral view has a more elliptical shape. The colour of the body is bright pink. Details of the labium, mandible and antenna are shown in fig. 4, c, d and e. The pupa has the peculiar structures on the dorsal surfaces of certain abdominal segments which may be seen in *Glyptotendipes glaucus*, but in *G. imbecillis* the 2nd segment does not bear one and they are present on the 3rd to 6th segments inclusive. The spines borne by the postero-lateral angle of the penultimate segment are shown in fig. 4, b.

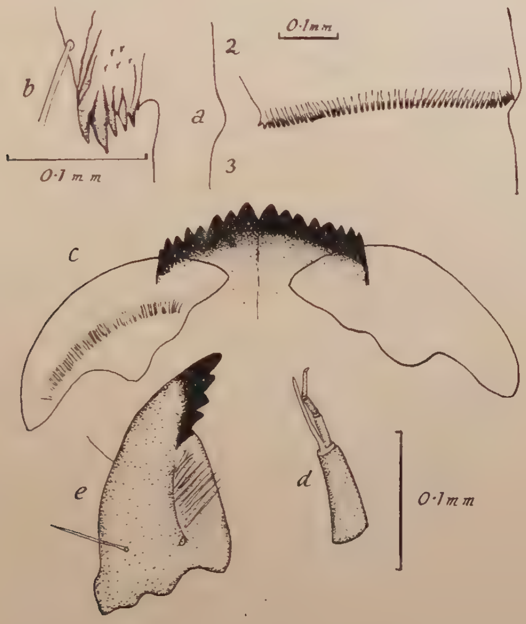

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FIG. 5.—*Pentapedilum tritum* (Walk.) pupal and larval characters. a. comb on 2nd abdominal segment of pupa; b. spines on penultimate segment of pupa; c. labium of larva; d. antenna of larva; e. mandible of larva.

There are two larvae in Gripekoven's account which closely resemble the above: *viz. Tendipes caulicola* Kieff. and *T. candidus* Kieff., and of these two *T. candidus* shows the more points of similarity to *G. imbecillis*. I note that, from the description of the adults, Edwards tentatively included *candidus* in *Glyptotendipes viridis* (Mcq.), which last is a species very similar to *G. imbecillis* Walk. and perhaps should not be separated from it. Goetghebuer included *candidus* in *Glyptotendipes severini* Goet., which again is very similar to *G. imbecillis*.

Some larval and pupal characters of *Pentapedilum tritum* (Walk.) are shown in fig. 5. The larva attains a length of about 7 mm. and is pale pink in colour.

The most noticeable larval character is the divided middle tooth of the labium. The pupa has very few characters which enable one to identify it easily. The spines on the angle of the penultimate segment are shown in fig. 5, b and a comb-like structure on the end of the second abdominal segment is drawn in fig. 5, a. Gripekoven referred to two species of *Pentapedilum,* of which one, namely *P. stratiotale,* is, judging from the characters of the pupa, very similar to *Pentapedilum tritum* : the structure of the larva is not described. Edwards (1929) tentatively included *P. stratiotale* Kieff. in *Pentapedilum tritum* Walk.

One may assume that the net-making habit is present in all the species of *Glyptotendipes*, and perhaps it is characteristic of all Chironomid larvae which make galleries in the tissues of water-plants. I have not yet succeeded in finding Chironomid larvae with similar behaviour among those which live in mud or among masses of algal filaments. In such cases the food is taken in directly from the substratum and although the body makes movements which drive water through the tube, the current so produced is not used to catch food, and presumably is essentially respiratory.

Case-making Chironomid Larvae.

Lauterborn (1905) described a number of oddly shaped cases made by Chironomid larvae recalling the cases of Caddis-fly larvae. Among them is one of a vase-like shape with arms spreading from the wider end. Lauterborn stated that these arms catch particles which drift past in the stream. Bause (1914) referred to these cases but doubted whether the arms are used to catch objects. Mundy (1909) gave some very minute observations on the behaviour of a case-making larva, but his work was printed privately and it escaped Bause's attention. Mundy described a larva under the name of *Chironomus pusio* Meig. which, from the morphology of its antennae, mandibles and labium, and from the shape of the case, agrees with the *Tanytarsus raptorius* Kieff. of Bause's account. Mundy described the building of the case in *Tanytarsus raptorius* and another larva in which the case is very similar but attached at the base by a stalk. Both these larvae live in rapidly flowing streams. Mud, cemented with silk, is gathered round the body to form the main part of the tube and then arms are made by sticking pellets of mud and silk one upon the other at points on the rim of the case. To make a net the larva runs up one of the arms, swings across to the next arm, carrying a thread of silk with it, and then moves across again, retreating as it does so until the space between the two arms is filled with a meshwork of threads. The net entangles particles from the moving water of the stream and from time to time the larva gathers up the region of the net lying between two arms and either eats it, or uses it for further building. This behaviour is reminiscent of that of the net-making Trichopterous larvae of the families HYDROPSYCHIDAE, PHILOPOTAMIDAE and POLYCENTROPIDAE, where a net is spun in front of the tube which entangles objects swept into it by the stream. There are, however, certain differences judging from the accounts of Wesenberg Lund (1911) and Noyes (1914). The net does to some extent entangle food in the form of diatoms but more typically it acts as a snare for larger organisms such as Ostracods, *Simulium* and Chironomid larvae; also the net is cleared of its contents by the larva going over it and is not periodically eaten and then respun.

Lauterborn (1905) also described several other peculiarly shaped cases which were made by Chironomid larvae living among the masses of vegetation in swamps, in particular one case-making larva which was figured by Réaumur

(1738). Bause (1914) referred to this larva as *Tanytarsus flexilis* and Edwards (1919) added further details of the eggs, early larval instars and form of the case. He called the species *Chironomus clavaticrus* Kieff. but later (1929) included it in *Lauterborniella marmoratus* (van der Wulp). The larva can move about in its case and protrude its head from either end: observations of its feeding habits would be interesting. The behaviour of *Glyptotendipes glaucus* Meig. and *Tanytarsus raptorius* suggest that there are probably other interesting methods of catching food among the larvae of the CHIRONOMIDAE.

I wish to thank Dr. W. H. Thorpe for his kind advice and criticism in the preparation of this paper; Dr. F. W. Edwards, F.R.S., for identifying material and Dr. A. Thienemann of Plön for assistance with the literature.

SUMMARY.

The larvae of *Glyptotendipes glaucus* (Mg.), *Glyptotendipes imbecillis* (Walk.), and *Pentapedilum tritum* (Walk.), make silk-lined tubes in the tissues of aquatic plants. The movements of the body of the larva cause a current of water to pass through the tube. The particles thus carried in are caught by a net which is periodically eaten with its entangled particles, and another one is spun in its place. The habit seems to be peculiar to those species living in water-plants. Attention is drawn to the peculiar cases made by certain Chironomid larvae which are referred to by various authors, and an account is quoted of a Chironomid larva, living in streams, which catches particles by spreading a net from the end of its tube.

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